Forced Migration and Population Expansion: The Genetic Story of the Garifuna

By
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Abstract:

The Garifuna are an admixed population that are found on St. Vincent Island in the Lesser Antilles and in over 60 villages in Central American, stretching along the coasts of Belize to Nicaragua. They were born out of admixture between the last native inhabitants of the Caribbean and escaped slaves. When Britain took control of the island in 1797, most Garifuna were forced to the island of Roátan, over 1,700 miles from their homeland. Roughly 2000 Garifuna survived war, disease, and deportation to Roátan. Today, over 300,000 Garifuna are estimated to live in Central America and large cities in the United States. Previous studies of Garifuna in St. Vincent and along the Central American coast have shown that the Garifuna are an admixed people with African, Native American, and some European genes. This work furthered these studies using uniparental markers, mitochondrial DNA and the non-recombining Y, to focus on some of the earliest Garifuna villages in Punta Gorda, Roátan and the Honduran Coast to better determine their origins and understand how a population adapts and expands in a new environment. Compared to the island of St. Vincent, coastal communities in Honduras have a reduced diversity and fewer native mtDNA or Y-chromosome haplotypes. Most mtDNA and Y lineages that are of African origin resemble West African regions from the earliest ports in the Atlantic slave trade, from Senegambia to the Bight of Biafra; however, there is evidence of origins from other parts of Africa. The mtDNA diversity in Garifuna Amerind Y haplotypes on St. Vincent appear most closely related to groups in South America, where the first peoples of the Lesser Antilles where thought to have originated. However, Y haplotypes from Honduras show that admixture with neighboring populations gave rise to half of the Y lineages belonging to native haplogroup Q. The lower diversity in the Garifuna is a sign of a population that has gone through multiple bottlenecks.

However, admixture with nearby groups, and an increase in migration in the Garifuna has worked toward increasing the diversity within Garifuna communities.

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This work is dedicated to Jeff, Mikah and Miles.

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Chapter 1: Introduction

The Garifuna (Garinagu or Black Caribs) of the Caribbean are an admixed population that occupy the islands of St. Vincent, and over 60 villages along the Central American Coast, stretching from Belize to Nicaragua. The Garifuna have always considered themselves as distinct from other African groups in the Caribbean and Central America. This distinction is evident in the telling of their origins, a tale of people that descended from the last resistance fighters against European occupation of their lands, and the Africans that succeeded in escaping slavery to join them. Many influences from South America, where Carib and Arawak groups that once lived in the Lesser Antilles are thought to have originated from, can be still be seen in their use of an Arawakan language, agricultural practices, and tools (Herrera-Paz, Matamoros, & Carracedo, 2010). More recently, as interest in migration to the United States has increased and more information about the African diaspora and American culture have become easily accessible, Garifuna have embraced their African origins (Talyor, 2012).

Garifuna villages are scattered along the Central American Coast along the Caribbean Sea. These villages are divided into sections of loosely organized households of related individuals. Each household is fluid, with members of an extended family moving between houses, with individuals appearing in a home for several weeks or months, then moving on to another family member or different work opportunity (Gonzalez N. L., 1984). Garifuna communities are matrifocal, where women are the center of the household and play a role in the preservation of culture and language. This role is a shift from their ancestors on St. Vincent, where a patriarchal society existed (Gonzalez N. L., 1984; Williams, 2014). This change was a response to a labor based economy that began shortly after their arrival in Central America, and

arose as the stressors of a loss of their people due to years of war and disease on St. Vincent combined with the pressures of adapting to new social and environmental factors (Gonzalez N. L., 1984). Brondo (2007) reported that 60% of homes owned by Garifuna were owned by women, with another 16% of the homes jointly owned. Many of these homes were passed down to women from their mothers. While the women are the center of Garifuna communities, most of the income in Garifuna economies come from labor obtained outside of the Garifuna village. Remittances from abroad have become increasingly important, making up all of the income of some Garifuna households (Brondo, 2007). Recent events have seen an increase in migratory movements for labor, further shuffling the genetic landscape of Garifuna villages.

One way to study the fission and fusion of a population, particularly when one or both of the sexes has a high rate of mobility, is through molecular studies. Uniparental markers have been used to answer questions of a population's origins and migration, as well as the mating practices and cultural norms that these practices are, or are not, adhered to. Mitochondrial DNA (mtDNA), a circular molecule found in the mitochondria of the cell, is passed on in a maternal fashion and can be used to elucidate the maternal origins and estimate the amount of admixture within a population. Similarly, the Y chromosome is largely non-recombining, and can be used to trace the paternal origins of a population. Both mtDNA and the non-recombining Y (NRY) chromosome contain portions that have a fast mutation rate, allowing for the examination of more recent history. This research utilizes mitochondrial DNA and Y chromosomal markers to better understand the following questions:

1) Who are the Garifuna of the Honduran Coast?

Research of the origins of the Garifuna began in the 1960s, and since that time it has become clear that the Garifuna are an admixed people of largely African and Native American origin, with some European input. Earliest admixture estimates were based on classical markers of Garifuna on the Central American Coast, which estimated African contributions of 64-75% and Amerindian contributions between 25-36%. On the island of St. Vincent, the admixture estimates were: African (41-51%) and Amerindian (29-53%) (Crawford, et al., 1981; Crawford, Dykes, Skradsky, & Polesky, 1984; Schanfield, Brown, & Crawford, 1984). It is clear that the composition of this admixture vary depending on the location of the group studied. Molecular markers allow for more refined questions, and allow for a closer examination of Garifuna origins.

Salazar Flores et al. (2015) used autosomal STRs to show that two distinct waves of slaves were brought to the Caribbean, the first from some of the earliest slave ports from Senegambia, the Gold Coast and the Bight Benin. Later arrivals were largely from the southeastern coast of Africa. Some of the earliest accounts of Africans in St. Vincent tell of a shipwreck, with survivors that made their way to the island and were welcomed by the Carib communities that lived there. Whether or not this tale describes the first Africans on the island, the first slaves to arrive in the Caribbean islands were sent from Western Africa. Gonzalez (1984), was able to document some Garifuna admixture with other Afro-Caribbean groups from Haiti and other parts of the Caribbean. If African genes were added in later admixture events, than the markers would resemble those from Western Central and Southern Africa, where the majority of later slaves brought to the Americas were acquired.

Additionally, further investigation of the origin of Native American lineages are examined by comparing maternal and paternal markers of the Garifuna to groups from South and Central America. In particular, mtDNA sequences and Y-STR haplotypes of Amerind origin are compared to Arawak and Cariban speakers from South America to test the hypothesis that Carib men took Arawak wives on the island. Previous studies in St. Vincent report that the Amerind component, both mtDNA and Y chromsosome, of the Garifuna most closely resembles haplotypes found in South America, particularly Brazil and Columbia, rather than groups in Central America (Benn Torres, et al., 2015). Because of this, admixture with Amerind and Mestizo groups in Central America were examined by comparing Garifuna lineages to neighboring communities where gene flow may have been possible.

2) What happens when a population expands rapidly and spreads across space?

The history of the Garifuna indicates that they underwent a major bottleneck from the island of St. Vincent, to the island of Roátan. Afterwards, Garifuna rapidly settled in different villages along the coast, and saw a rapid increase in population size. In Honduras, Garifuna now occupy over 50 communities that range in size between 1,500 and 4,000 inhabitants, many of which were established in the first 50 years of settlement in the Central American Coast. (Herrera-Paz E. F., 2017). The repeated founder effects that occurred as new villages arose would likely increase the genetic diversity between villages, while decreasing the amount of variation within each village (Corre & Kremer, 1998). The amount of diversity found in the coastal populations would be influenced by the size of the population, gene flow between the

coastal communities, and the resources available that can sustain the community through population growth (Corre & Kremer, 1998).

Genetic drift would decrease the diversity within each village, but more recent events that have encouraged gene flow would increase the diversity and add new genes to the community pool. Seasonal migration in Central America began in the 1800s. After World War II, the United States began to become a source for jobs. The paving of roads along the Honduran coast over the last generation further increased the rate of migration, particularly of males looking for work in the west, out of Trujillo and Santa Fe. Trujillo was the earliest site of Garifuna settlement on the Central American coast, but as economic conditions shifted in the region, labor opportunities lessened, and many Garifuna have migrated out of the city (Herrera-Paz E. F., 2017). Until the last few decades, the income received through this labor migration was meant to supplement the Garifuna subsistence economy, and act as a cultural barrier to changing economic conditions (Brondo, 2007). However, a change in legal practices leading to loss of Garifuna land to the tourism industry has caused this migratory labor practice to shift from being a supplement to providing a major part of the Garifuna economy. In 1992, a law was passed in Honduras that made it easier for foreign investors to purchase plots of land, encouraging the exploitation of Garifuna land for tourism. Additional stress has been placed on Garifuna communities, as catastrophic environmental events such as Hurricane Mitch (1998) and Tropical Depression Gamma (2005) have displaced individuals and disrupted social networks that act as an economic safety net (Wrathall, 2012). Garifuna, already matrifocal, have seen an increase in turning to elder women in the communities to care for children while men, and increasingly women, seek labor from outside sources. As these cultural events unfold, they reshape the biological structure in Garifuna communities.

From the founding group of 2000 Garifuna, to the more recent episodes of forced migration, the Garifuna have been a population in constant adaptation to environmental stressors. The cultural responses to these stressors have biological consequences, and using molecular markers this project examines the genetic composition of these communities and examines how they compare to neighboring groups. The use of uniparental markers allows for a comparison of the differences that occurred between the sexes within Garifuna villages in Honduras.

The following work is divided into five additional chapters that try to put these questions into context and explain the methods used to answer them. Chapter 2 provides a history of the Garifuna, and the biological research that has been done to examine questions of Garifuna origin. Chapter 3 details the methods used in sample and data collection, and explains the laboratory and statistical methods utilized. Chapter 4 provides results from the laboratory and statistical methods described in Chapter 3. A discussion of these results, and how they answer the above questions are provided in Chapter 5. And finally, Chapter 6 summarizes the findings of this study.

Chapter 2: The History of the Garifuna

The Garifuna were born on the island of St. Vincent when the first escaped African slaves settled in communities with the Native Caribbean peoples that occupied the island, around the early 1600s. Over the next 200 years, most of the Garifuna would be forcibly removed from St. Vincent and resettled over 1,700 miles away on the island of Roátan, off the Honduran Coast. The Garifuna are a relatively young ethnic group that has been in existence for some 400 years. This chapter describes the events and biological consequences that created the Garifuna, and led them from a small group of around 2000 individuals to over 300,000 people occupying villages all along the Central American coast, as well as major Central American and North American cities.

The Peopling of St. Vincent Island

The Garifuna story begins in the Lesser Antilles, an area of islands that stretch 950 km between the Caribbean Sea and the Atlantic Ocean (Figure 2.1). St. Vincent, called *Youromaÿn* by the inhabitants living on the island during European contact, is one of the larger islands (352.7 km^2) in this island arc system, with a young geological age and frequent volcanic activity (Talyor, 2012; Callaghn, 2007). The island is a part of the southern Windward Islands, islands that lie south of Dominica stretching towards Trinidad (Fitzpatrick, 2015). St. Vincent has a rugged terrain, with forested mountainous regions, and fertile land found at areas below 200 meters above sea level (Callaghn, 2007).

Figure 2.1. St. Vincent and the Greater and Lesser Antilles Islands of the Caribbean.

While many islands in the Greater and Lesser Antilles begun to be settled around 8000 years B.P., the first evidence of human settlement in St. Vincent and much of the southern Antilles were did not appear until around 2000 calibrated (following radiocarbon dating to better represent calendar years) years B.P. (Benn Torres et al., 2007; Fitzpatrick, 2015). Evidence of occupation in St. Vincent appears even later, around 1650 calibrated years B.P. (Fitzpatrick, 2015). This time period, the Ceramic Age, was a time of population dispersal throughout the Caribbean associated with a cultural complex known as the Saladoid complex. The late occupations of the southern islands were accompanied by root crop horticulture, use of land and ocean animal resources, pottery, a wide range of craft working including wood, stone, bone and shell, and a technology that used ceramic vessels to create freshwater wells (Fitzpatrick, 2015; Reid et al., 2014). On St. Vincent, early settlement sites have been found on low elevation coastal areas or in the secondary forest towards the southwest portions of the island (Fitzpatrick, 2015; Callaghn, 2007).

The origins of groups living on St. Vincent and other islands in the Lesser Antilles upon European contact is unclear. Earlier research in the area pointed to the origin of the Saladoid complex in the Orinoco River Basin of Venezuela, a complex that later, around 2500 cal yr B.P., spread in a stepping-stone model of occupation throughout the Caribbean (Fitzpatrick, 2015; Reid et al., 2014). However, it now appears that occupation of the islands was more complicated and varied based on previous occupation, resources of each individual island, technologies available to access those resources, and accessibility of the island as a result of distance and ocean currents (Fitzpatrick, 2015). These factors, coupled with increased sociopolitical complexity and more developed trade systems, meant that the peopling of St. Vincent probably occurred during multiple stages as the result of movements of people from both Central and South America.

Who Are The Island Caribs?

Until the 1980s many scholars believed that the Island Caribs, a term commonly applied to all Amerindian islanders in the Caribbean, were decedents of a group of invaders that had moved into, replaced, or conquered islands in the Lesser Antilles by 1220 A.D. (Bullen & Bullen, 1972). Gonzalez (1984) noted that the use of different languages by men and women on St. Vincent had often been used as an argument for this hypothesis. Migration myths recorded by the earliest European writings also supported this idea. The first Europeans to reach the Lesser Antilles described two distinct groups, Arawak speakers and Island Caribs (Mendisco, et al., 2014). Father Breton, a missionary on the island during the 1600s, recorded a migration myth that suggested that these people were descendants of *Kalinago,* who came with his family from Guyana and conquered the Arawak peoples that originally lived in the islands (Allaire,

1980). However, archaeological and linguistic evidence now puts the idea of an invading force into doubt.

Around 1500-1400 cal yr B.P., a new ceramic tradition emerges in the Caribbean called the Troumassoid. Initially, the appearance of new ceramic cultures were argued to be an influx of new peoples arriving from South America (Reid, Hofman, Gilmore III, & Armstrong, 2014). Today it is believed that these traditions were developed locally, within the communities in which they were found, and the geographic distribution of similar styles is a result of greater interaction with peoples from the mainland and other islands. For examples, the Cayoid series of pottery can be found, not only on St. Vincent, but also on Dominica, Grenada, Guadeloupe, Martinique, St. Lucia, and Trinidad. A similar style of pottery was found in the Guianas, but this evidence appears later in the archaeological record (Fitzpatrick, 2015). This suggests that rather than this style arriving in the Caribbean islands with people migrating from the South American mainland, that it originated in the islands themselves and later spread to other parts of the region.

Linguistic evidence has also been used to argue for the arrival of new peoples that would eventually take over the lands of the Arawakan speaking peoples. This argument relied on research done by Father Breton who tried to compile a dictionary of the Carib language. Father Breton found that the men and women of Dominica used different languages (Talyor, 2012). The women's language has been shown to belong to the Arawak language group, and this was argued to be evidence of a Carib invasion where the Carib speaking men took on Arawak speaking wives. Breton's work actually suggests that the Islanders spoke three different languages or dialects, one by the women, one by men, and another that was used by warriors and during ceremonies (Talyor, 2012). Review of the work shows that the women's language was derived from Arawakan, a language that shares a common origin with Taino and some South

American languages, with a large vocabulary that included borrowed words from Cariban. The men's language, while using some borrowed elements and words from mainland Cariban, also used an Arawakan grammar and has been characterized as a Carib pidgin. These findings could suggest that the users of the male language were not Carib raiders, but rather used this language for when interacting with people on the mainland and other islands. In other words, the use of this other tongue was to support trade as groups moved throughout the islands of the Caribbean (Davis & Goodwin, 1990).

Some have also argued that Father Breton's evidence, recorded on Dominica, may not pertain to the inhabitants of St. Vincent. St. Vincent Caribs claimed that they were in alliance with Cariban speaking groups, an alliance that included marriages (Davis & Goodwin, 1990). Others have argued that all Island Caribs were decedents of Arawakan speakers that lived in the Windward Islands for hundreds of years before the arrival of the European, but these people maintained relations with the mainland through trade, intermarriage, and military alliances (Davis & Goodwin, 1990). These alliances would prove important as Taino groups in the Greater Antilles begin to have a more influence throughout the Caribbean by the time Europeans made first contact (Fitzpatrick, 2015). In short, the people of the Caribbean may have had a higher rate of gene flow, without necessitating the takeover of lands, between neighboring groups than early descriptions first imply.

European Conquest and the Atlantic Slave Trade

In the late 1400s, expeditions seeking a maritime route to India and the East Indies began departing from Europe and heading south and west. Within the five years between 1487 and 1492, Europe would discover a New World and a southern route along the coast of Africa that

could provide a source for African slaves that could be used to exploit this New World (Thomas, 1997). European explorers first made contact in the Caribbean when Christopher Columbus, under a Spanish flag, arrived in 1492. The first African to reach the New World may well have been a part of one of Columbus's first few voyages (Thomas, 1997). In these early years, Caribbean slaves were gathered from the islands, and some were sent back to Spain. However, problems with forced labor amongst the Native Caribbean populations soon arose, and by 1501 Spain had forbade Native Caribbean slaves to be sent to Europe (Thomas, 1997). By 1503, the Spanish crown begun to claim regions within the Caribbean islands, including St. Vincent. Sugar cane was being grown in the Caribbean as early as 1505, and the first mines were established five years later. This type of work was physically demanding and it soon became evident that islanders were not used to this type of labor, and they were susceptible to the many new diseases being brought by the Europeans. The demand for African slaves rose rapidly (Thomas, 1997).

By the early 17th century, the Dutch, French and English began to show interest in the settlement of Carib territories (Talyor, 2012). The Caribs of St. Vincent and Dominica managed to resist European control until 1668 when they signed a peace treaty with the French and English, allowing them to settle their islands with the understanding that these islands were Carib by right (Anderson, 1997; Talyor, 2012). By this time, the other Caribs of the Caribbean had nearly disappeared following warfare, disease, famine, and enslavement. The islands of St. Vincent and Dominica were the last major areas of Native Caribbean occupation (Monsalve & Hagelberg, 1997; Mendisco, et al., 2014).

It did not take long for this peace to waiver, and by 1674 the Caribs formed an alliance with the French and worked towards disrupting English attempts at Caribbean settlement on Antigua and Montserrat. English attempts to build settlements on St. Vincent failed, and by

1719 not one could be found (Talyor, 2012). The French, on the other hand, had several settlements on the island, and by 1729, an estimated 300 individuals were residing on St. Vincent (Talyor, 2012). The alliance with the French continued even as the English would claim rights to the island again some 50 years later. However, by 1815 the English had placed a lasting claim to St. Vincent and Dominica (Talyor, 2012; Benn Torres, Kittles, & Stone, 2007).

African Arrival: The Birth of the Garifuna

The African slave trade began shortly after discovery of the Caribbean, and by 1850 more than 12 million Africans had been carried to the New World, some 2 million to the British Antilles and 28,000 to the Danish Antilles (Schroeder, et al., 2015; Thomas, 1997). On St. Vincent, Africans began arriving by shipwreck, raids on neighboring islands, and through escape from their masters (Crawford M. H., 1984). The earliest reference of Africans on the island comes from an English letter in 1596, which mentions "one of their [Indians] slaves" (Talyor, 2012). As early as the 1660s, English records often described two distinct populations on St. Vincent consisting of "Black" Caribs and of "Yellow" or "Red" Caribs (Talyor, 2012).

There are several reports of shipwrecks throughout the region, which may have led to the arrival of Africans on the island of St. Vincent. An English governor in 1667 claimed that two Spanish slave ships from Guinea wrecked in 1635, and some surviving slaves made it to St. Vincent. Another account notes that the ship was Dutch or English, arguments that would allow for the recapture of the surviving slaves. However, in the mid-1700s a Black Carib chief noted that the ship was Spanish (Talyor, 2012). Other accounts include a wrecked slaving ship in 1675, that was believed to be from the Bight of Benin in West Africa, and wrecked off the coast of Barbados during a year that a hurricane struck (Firschein, 1961; Talyor, 2012). Two British

governors of St. Vincent reported the same ship but their dates differ from the previous accounts, dating the wreck at 1712 or 1734, and claimed the ship wrecked on the windward part of St. Vincent. Hurricanes and hazardous conditions often resulted in shipwrecks in the region and these accounts may reflect several wrecks on or near the island (Talyor, 2012). They may also be later attempts to describe the numbers of Africans that were living in St. Vincent by the mid-1700s. A report in 1676 claimed that there were around 3000 Black Caribs residing on the island (Crawford M. H., Problems and Hypotheses: An Introduction, 1984).

The composition of these early African arrivals notes some discussion. First, the earliest wave of African slaves were from West Africa, in the Senegambia and Bight of Benin region, where the Portuguese has established some of their earliest depots that provided the majority of slaves until the 1550s (Thomas, 1997). Other coastal regions, including the Congo, Angola (West Central Africa) and Mozambique (Southern Africa), would not be exploited until later (Salas A. , et al., 2005). Second, importation of slaves throughout the slave trade generally favored males over females (Salas A. , et al., 2005). However, French reports of shipwreck survivors notes that both men and women survived (Talyor, 2012). Early colonizing regions, such as Jamaica, St. Kitts and Barbados had more female than male Africans, so you would expect a large African contributions to the maternal gene pool of St. Vincent (Benn Torres, Kittles, & Stone, 2007).

Table 2.1. Estimated number of slaves brought to the Americas from each major slave port region (Thomas, 1997).

Slave port	Number
Senegambia	2,000,000
Windward Coast	250,000
Ivory Coast	250,000
Gold Coast	1,500,000
Bight of Benin	4,000,000
Bight of Biafra	250,000
West Central Africa	3,750,000
Southern Africa/Madagascar	1,000,000
Total	**13,000,000**

Another source of Africans that could contribute to the Black Carib population may have come from Carib raids on other European controlled islands. A report from the late 1500s described a raid on the Spanish settlements in the Greater Antilles, which included the capture of African salves that were either left in Dominica or dispersed among other Carib settlements (Talyor, 2012). By 1612, as many as 2000 African slaves could have been brought into Carib territories (Thomas, 1997). Carib raids in the 1650s included not only African slaves, but also English men, women and children, some 300 of which were held in Dominica (Talyor, 2012).

Escaped slaves that made their way to Carib territories also contributed to the Black Carib population on St. Vincent. In 1776, St. Vincent had over 10,000 slaves under English control. Some 1,200 of these slaves were labeled as runaways and presumed to be living with Caribs on the island. The prevailing current also influenced the number of escaped slaves that reached St. Vincent. A group of slaves from Barbados could locate a boat that would carry them all the way to the island without navigation (Talyor, 2012). The acceptance of runaway slaves varied through time by the practices of local chiefs and the availability of resources (Talyor, 2012; Anderson, 1997). In general, however, the presence of African slaves were preferred to the European powers that tried to control the island (Anderson, 1997).

Once Africans began to settle in Carib territories they soon adopted their Carib cultural practices and often intermarried with the island's inhabitants (Salas A. , et al., 2005). Diet, language, lifestyle and even the practice of head deformation, a practice that identified them as Carib instead of slave, was seen in early Caribs of African descent (Salazar-Flores, et al., 2015; Talyor, 2012). This complete adaptation to Carib way of life, with little African influences, may show that Africans were incorporated slowly and over a long period of time (Gonzalez N. L., 1984). It may also reflect a need to appear "Carib" in order to claim rights to Carib lands.

Conflict and War

Relationships between the Island Caribs and Africans that had made their way to St. Vincent were not always peaceful. French records during the early 1700s indicated tension between the two, sometimes distinct groups, with Black Caribs claiming the windward coast and the Island Caribs staying on the leeward coast. Some skirmishes between the two groups were noted in 1707. As the Black Carib population rose in numbers, Island Caribs were on a steady decline. By 1777, a governor estimated that the Black Carib population was around 4,000 but the Island Caribs were only around 40 (Talyor, 2012). However, it is unclear if this decline was due to an increase in individuals due to African admixture, deaths due to European diseases, or violence.

Tensions with European powers also continued to simmer. In the 18th century, England tried to characterize the Black Caribs as runaway slaves. The Black Caribs, on the other hand, stressed that they were Island Caribs through admixture and that they had the rights granted to the Island Caribs through various peace treaties (Talyor, 2012). These tensions were in part due to the Carib resistance towards building sugar mills on the island, a practice that destroyed the

land and required a large body of slave labor. The loss of land, the stronger influence of the British, a severe hurricane that struck in 1780, famine, and small pox put further pressure on the Black Caribs on the island.

In 1784, the Treaty of Paris once again placed control of the island firmly in British hands, and because the Black Caribs had fought fiercely as allies to the French, the British crown was not as willing to allow them hold of their lands. The independence of the United States left British loyalists without a place of refuge, and talks of moving the Black Caribs from St. Vincent to the island of Bequia began to win favor (Talyor, 2012). When news of France once again going to war with Britain reached the Black Caribs, hopes that they could reclaim their land were renewed. While making promises to Britain that they would remain neutral, they soon sought out French allies on Martinique. In 1796, under the Black Carib Chief Chatoyer, the Black Caribs began attacking and burning the English lands on St. Vincent. In the end, the Caribs would lose both their leader and the war, and by June of 1796, the war between France and Britain ended.

Deportation and the Settlement of the Central American Coast

The first group of Black Caribs, some 276 individuals, were moved to the island of Baliceaux in July of 1796 (See Figure 2.2). As more individuals surrendered or were captured the Black Carib population on Baliceaux grew, and by October the number had grown to 2,664 individuals. Within six months, a total of 4,633 individuals (1,080 men, 1843 women, and 1643 children) were confined to the island (Talyor, 2012). The numbers continued to rise as more groups were brought over from St. Vincent and, by some higher estimates, as many as 5,500 Black Caribs had been transported to Baliceaux by March of 1797 (Talyor, 2012).

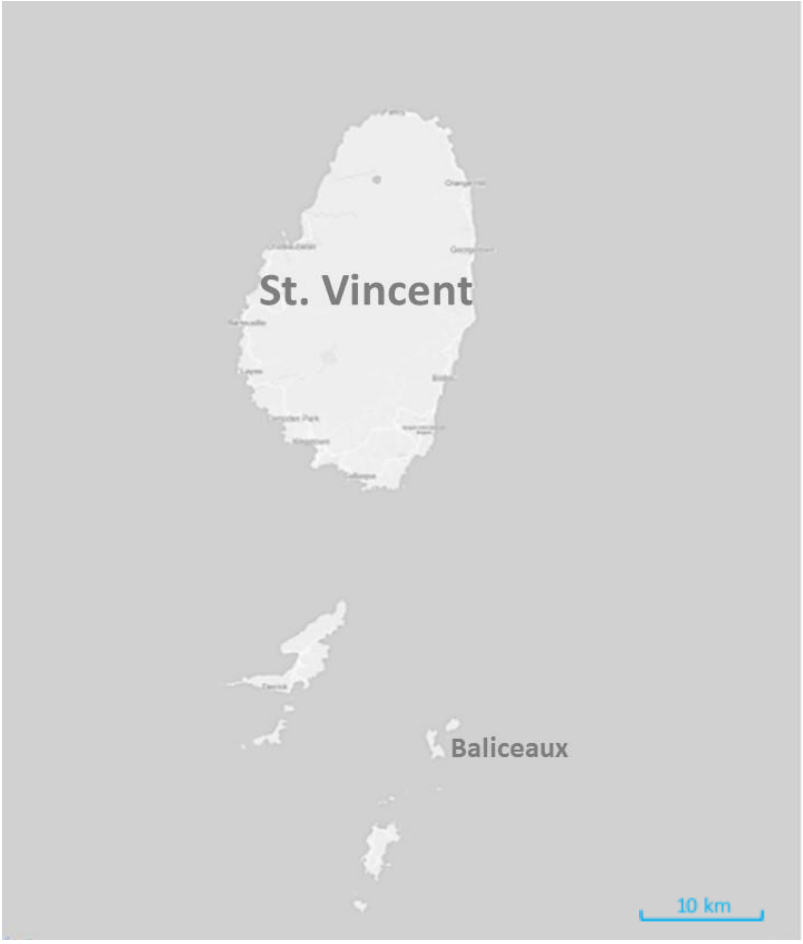

Figure 2.2. The islands of St. Vincent and Baliceaux.

The conditions on Baliceaux were not adequate towards provisioning the number of prisoners it held. Baliceaux is a small island south of St. Vincent, roughly 0.8 km^2, has no fresh water and little vegetation or arable soil (GIPSVG Inc., 2015). The Black Caribs arriving on the island were already malnurished following warfare and forced hiding from British forces, and the conditions on Baliceaux did little to aid in their recovery (Talyor, 2012). In August, disease began to spread throughout the Caribbean with some 80,000 reported cases. The epidemic was described as a "malignant pestilential fever," and descriptions have led some researchers to believe that it may have been Yellow fever or typhus (Talyor, 2012; Gonzalez N. L., 1984).

Within a month after the disease hit Baliceaux, 12 Black Caribs died. The following month, 100 individuals died of the disease, and by December 950 Black Caribs had fallen to the disease (Talyor, 2012).

As conditions on the island worsened, the British decided it was time to move the Black Caribs to a more permanent settlement. In March of 1797, the survivors departed Balicaeux. Only 2,248 survivors remained to leave the island. In route to their new destination, one ship, the *Prince William Henry*, was lost to the Spanish. Finally, on April 11th, the Black Caribs of St. Vincent had sighted the island of Roátan off the coast of Honduras (Talyor, 2012) (See Figure 2.3). Some 2,026 individuals, 664 men and 1,362 women and children were left on Roátan, where the British thought they would remain (Gonzalez N. L., 1984; Talyor, 2012).

A brief survey of Roátan revealed an island poor in resources, and the Garifuna soon set their sights on the Honduran coast (Gonzalez N. L., 1984). Negotiations began with Spanish colonial officials in Trujillo, Honduras, and by May an agreement had been made. The result of these talks led to a large movement of Black Caribs to Trujillo, where they establishd the earliest communities in Rio Negro and Santa Fe. By September, 1797, 1,465 Black Caribs were living in Trujillo. By the following October, only 206 Black Caribs remained on Roátan (Talyor, 2012).

Figure 2.3. Map of Roátan off the Honduran coast in relation to the rest of the Caribbean.

The use of Biological markers in Anthropological Studies

Because of the spread of the Garifuna population, different historical, social, and environmental factors have been at work shaping the genetic makeup of each community. These microevolutionary differences have been investigated since the 1950s, when the first researchers began gathering blood, demographic, and anthropometric data in the Caribbean, in attempts to determine the origin of the Garifuna and other African descendant groups in region. Various measurements of morphological variation have also been used to study origins and admixture within and among populations in the Caribbean. These measurements include odontometerics and the study of discrete dental traits (O'Rourke, Baume, Mielke, & Crawford, 1984), anthropometrics (Lin, 1984), and dermatoglyphics (Lin, et al., 1984). The following summarizes the biological markers used in these studies, some of the historical factors that have shaped each community, as well as the research and findings of studies undertaken in each region (See Table 2.2 for a summary).

Ludwik and Hanka Hirschfeld first described variation that they observed in humans in regard to the ABO blood group system, through their work during World War I. Soon after, other blood group systems began to be described such as the Rhesus, MNS, Duffy and the Diego systems, all of which displayed variation within human populations (Crawford M. H., 2007). Studies of classical markers in the Caribbean began during the 1950s, soon after the sickle cell trait had begun to be suspected in protecting individuals from the *plasmodium falciparum* parasite (Firschein, 1961). Other polymorphisms were studied including various blood group and hemoglobin polymorphisms, red cell enzymes, plasma and serum proteins, and immunoglobulin allotypes (Crawford M. H., 1984; Custodio & Huntsman, 1984; Crawford, 1983; Weymes &

Gershowitz, 1984; Crawford, Dykes, Skradsky, & Polesky, 1984; Schanfield, Brown, & Crawford, 1984; Devor, Crawford, & Bach-Enciso, 1984).

In the 1980s, researchers were beginning to use molecular markers to answer questions of human ancestry. The first molecule that was commonly used to answer anthropological questions was mitochondrial DNA (mtDNA), which was first sequenced in 1981 (Crawford M. H., 2007). Unlike nuclear DNA, mtDNA is not found within the nucleus of the cell, and is instead found within each of a cell's mitochondria. For every copy of nuclear DNA, there are hundreds to thousands of copies of mtDNA (Rubicz, Melton, & Crawford, 2007). MtDNA is a double stranded, circular molecule made up of 16,569 base pairs that largely code for protein (Cann R. , 1988; Pakendorf & Stoneking, 2005). The coding portion of mtDNA has a rapid mutation rate between 5 to 10 times faster than that of nuclear DNA, at 0.017×10^{-6} substitutions per site per year (Pakendorf & Stoneking, 2005). The molecule is particularly interesting to questions of human origin because it is inherited in a maternal fashion and does not recombine (Giles, H, Cann, & Wallce, 1980). These features mean that the molecule is identical by descent, allowing researchers to trace the maternal ancestry of a population, utilizing a growing list of catalogued mutations that are found within populations worldwide (Cann R. , 1988; Jobling, Hollox, Hurles, Kivisild, & Tyler-Smith, 2014).

Table 2.2. Summary of research on the Garifuna and Black Caribs of the Caribbean.

Source	Location	Type of Research	Summary
Firschen 1961	Stann Creek, Hopkins and Seine Bight, Belize	Blood Group Polymorphisms	A high frequency of the sickle-cell trait (0.241) indicates a West African ancestry; evidence for Native Ancestry in the Di^a Diego allele (0.016) and R^z allele of the Rh bollod group system. Differentiation between sites show evidence of founder effect.
Crawford et al. 1981	Livingston, Guatemala	Blood Group. Red Blood Cell and Serum Protien Polymorphisms	Estimated admixture using 24 classical polymorphism estimated that Livingston Garibs had parental contributtions of: African (70%), Native (29%), and European (1%).
Lin 1984	Sandy Bay, Owia, and Fancy, St. Vincent; Livingston, Guatemala	Anthropometrics	Body shape and size are under different b/t St. Vincent and Livingston Caribs due to variation in genetic admixture and differences in environment, diet, and labor.
O'Rourke et al. 1984	Dangriga and Punta Gorda, Belize	Dental Variation	Relatively little variation seen between two Black Carib groups and a Creole group.
Lin et al. 1984	Livingston, Guatemala; Belize City, Belize; Corozal and Sambo Creek, Honduras	Dermatoglyphics	Differences in patterns by sexes, with the relationship between measures showing a higher relationship with geography in female samples (r=0.64) *vs.* males (r=0.38).
Wyems & Gershowitz 1984	Hopkins, Stann Creek, and Punta Gorda, Belize	Hemoglobins, Red Cell Enzymes and Serum Proteins	Found that the villages of Punta Gorda and Hopkins were more genetically similarbased on 8 markers; Stann Creek and Seine Bight clustered together.
Custodio et al. 1984	Punta Gorda, Belize; Limon, Honduras	Blood Group, Hemoglobin and Plasma Protein Polymorphisma	Found that most frequencies of polymorphisms are intermediate to those found in Native and West African populations; founders effect and natural selection probably play a role in the differentiation of villages.
Custodio & Huntsman 1984	Corozal, Santa Rosa de Aguan, Limon, and Tocamacho, Honduras; Punta Gorda, Roatan; Stann Creek and Seine Bight, Belize	Abnormal Hemoglobins	Sickle cell carriers were found in 12.1% of the 1750 individuals in the study, with the highest rate (18.9) seen in Seine Bight, the lowest found in Santa Rosa de Aguan (6.1%).
Crawford et al. 1984	Livingston, Guatemala; Stann Creek and Punta Gorda, Belize; Sandy Bay and Owia, St. Vincent	Blood Group, Serum Proteins and Red Cell Enzyme Polymorphisms	Admixture estimates to determine African *vs.* native ancestry indicated that the highest proportion of African genes were found in Livingston, Guatemala, and the lowest found in Sandy Bay.
Schanfield et al. 1984	Sandy Bay, St. Vincent; Stann Creek, Belize	Immunoglobulin Allotypes	Compared Black Caribs and Creoles of Belize and St. Vincent and found that the highest frequency of Native markers were in the Caribs of Sandy Bay, St. Vincent. European admixture estimates were high in the Punta Gorda Creoles of Belize, but little European markers are found in Carib groups.

Source	Location	Type of Research	Summary
Devor et al. 1984	Crawford et al. 1984; Weyemes and Gershowits 1984; Custodio et al. 1984	Population structure	Black Caribs are distinct from other Afro-Caribbean populations, as well as differ between villages due to extensive migration, founder effect, and admixture with nearby groups. Coastal villages near larger cities appear more admixed, whereas issolated villages along the coast have less diversity. The largest amount of native genes are found in St. Vincent.
Monslave & Hagelberg 1997	Belize	MtDNA	MtDNA analyses revealed high levels of West African mtDNA lineages, withsomeone of the 28 individuals having a haplotype found in native populations.
Salas et al. 2005	Honduran coast	MtDNA	Compared the mtDNA of Garifunas from Honduras and Chocó from Columbia and found that both populations have a strong Africa component, with the Garifuna exhibiting signals of founder effect.
Herrera-Paz et al. 2008	Bajamar, Iriona, and Corozal, Honduras	13 Autosomal STRs	Results indicated a high level of heterozygosity in the 13 loci studied, with a strong African component present.
Herrera-Paz et al. 2010	Bajamar, Corozal, and Iriona, Honduras	13 Autosomal STRs, Isonymy, Migration Matrices	Indicates an increase of migration over generations, with a general movement from east to west and neolocality shifting into a matrilocal pattern. Garifuna clustter with other Afro-Caribbean and African populations when compared to populations from the Americas, Africa and Europe.
Phillips-Krawczak 2012	Fancy, Owia, Sandy Bay and Greiggs, St. Vincent; Punta Gorda and Barranco, Belize; Carib Indian Reserve, Dominica	MtDNA and Y STRs	Study found higher diversity in St. Vincent and Dominica when compared to the villages in Belize, indicative of genetic drift following several founder events.
Herrera-Paz 2013	26 Garifuna Villages on the Honduran Coast	Isonomy	Genetic distances calculated from isonomy indicate short pairwise distance among communities and a positive correlation with geographic distance.
Salazar-Flores et al. 2015	Compared Herrera-Paz et al. (2008) to otther groups in the Carribean	13 Autosomal STRs	Comapared Mexican Mestizos to other popluations in Latin America and the Caribbean and found that the Garifuna of Honduras had on of the highest levels of African ancestry. Study also found two pulses of slave migration, the first from the West Coast during early slave trade and the second from West Central Africa that occurred during the later part of the slave trade.
Benn-Torres et al. 2015	Kingstown area, St. Vincent	MtDNA, Y chromosome, and Autosomal STRs	St. Vincent Garifuna have a high frequency of mt DNA haplogroup C1 and a lower frequency of haplgroup A2 (combined 46%) and Y haplgroup Q. Data from this study supports the origin of native DNA from northern South America rather than a Central American origin.

Outside of the coding regions of the mitochondrial genome, in a part called the control region or d-loop, lies a segment of DNA that mutates at an even faster rate and has provided scientists with information on historical events in human history (Pakendorf & Stoneking, 2005). Within this control region are two segments, the hypervariable segment I (HVS-I) and hypervariable segment II (HVS-II) that, by phylogenetic comparisons, mutate at 0.075-0.165 x 10^{-6} substitutions per site per year, or by pedigree analysis, average 0.47 x 10^{-6} substitutions per site per year (Pakendorf & Stoneking, 2005). This additional information has allowed to further classify mtDNA genomes into subclades that can be traced to different regions of the world.

The Garifuna are believed to be the result of admixture between three major groups: Native American, European, and African. Each major group has mtDNA haplogroups that are commonly found within them. Haplogroups A, B, C, D and a specific subtype of haplogroup X are found in the Americas and display a latitudinal gradient with an increase in haplogroups C and D southward, and an increase in haplogroup A the farther north the population is located (Lalueza Fox, 1996). In Europe, haplogroup H is most prevalent and found between 40-50% in all European populations (Achilli, et al., 2004). Nine other haplogroups are found in Europe including: U, T, K, J, X, I, V, W and M (Finnila, Hassinen, Ala-Kokko, & Majamaa, 2000). Most African lineages belong to the macrohaplogroups L0-L3, with L2 being the most commonly found haplogroup that spread from Western Africa to Eastern and Southern Africa around 70-50 kya, and then spread throughout the rest of the African continent following the Bantu expansion (Silva, et al., 2015). Haplogroups L1c and L3e are also found at high frequencies in Western Africa (Silva, et al., 2015) (Figure 2.4).

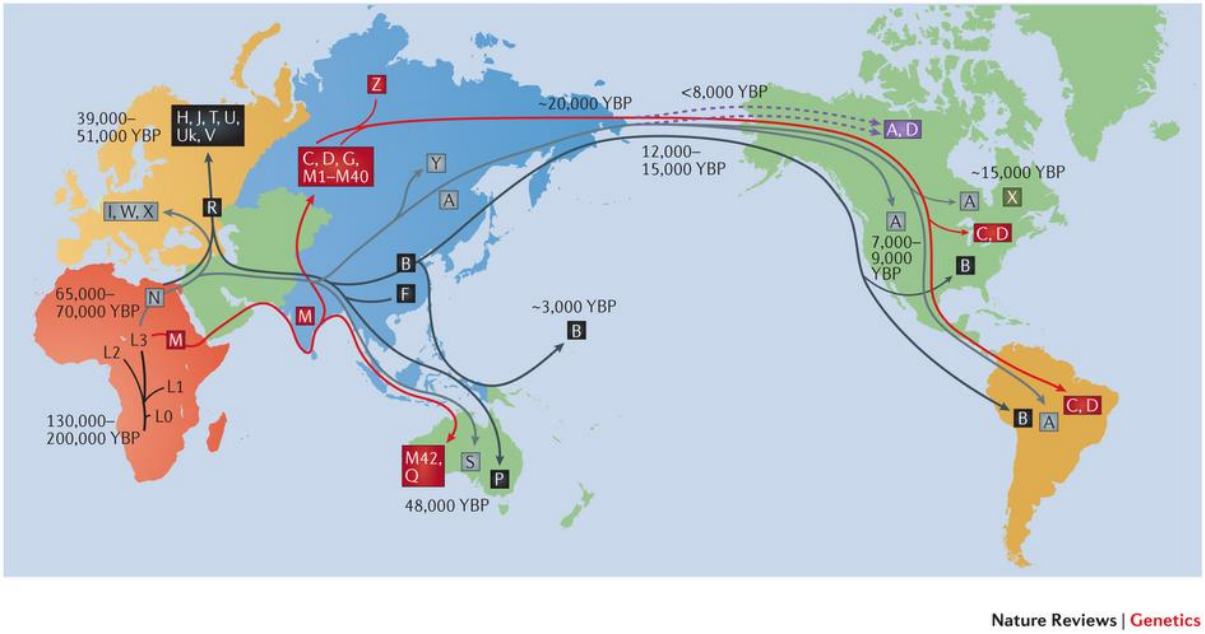

Figure 2.4. Map of mtDNA haplogroup migrations throughout the world (Stewart & Chinnery, 2015).

Y chromosome markers have been found to strongly correlate with geography making them useful in inferring population history and migrations (Rosser, et al., 2000). A large portion of this 60 million base long chromosome, roughly 95% of the Y chromosome, is non-recombining (NRY) (Tilford, et al., 2001; Novelletto, 2007). Similar to mtDNA, which provides information on the maternal history of a population, the paternally inherited NRY provides information on the paternal history of a population (Novelletto, 2007). A combination of slow mutating single nucleotide polymorphisms (SNPs) and faster mutating segments of DNA, called short tandem repeats (STRs), are found in the NRY and have been used to classify the worldwide Y chromosomal variation into major haplogroups and subclades (YCC, 2002; Karafet et al., 2008). SNPs are changes at a single base that mutate at the relatively slow rate of about 10^{-8} per base pair per generation (Novelletto, 2007). Because of this, SNPs are better for tracking prehistoric changes, while STRs can give information on more recent events (Roewer, et al.,

2005). Mutations in STRs consist of additions or deletions of a repeated segment of DNA that occur at rates 10^5 to 10^6 times faster than mutations in other parts of the Y chromosome (Roewer, et al., 2005). Attempts at assigning an average rate of Y STR mutation yield an average mutation rate between 2.1 x 10^{-3} and 3.35 x 10^{-3} per marker per generation, faster than the mutation rate found in the hypervariable regions of mtDNA. Also, the rates vary greatly among individual loci so it is important to understand the rates of mutations for each loci being used (Hohoff, et al., 2007; Ballantyne, et al., 2010; Kayser & Sajantila, 2001).

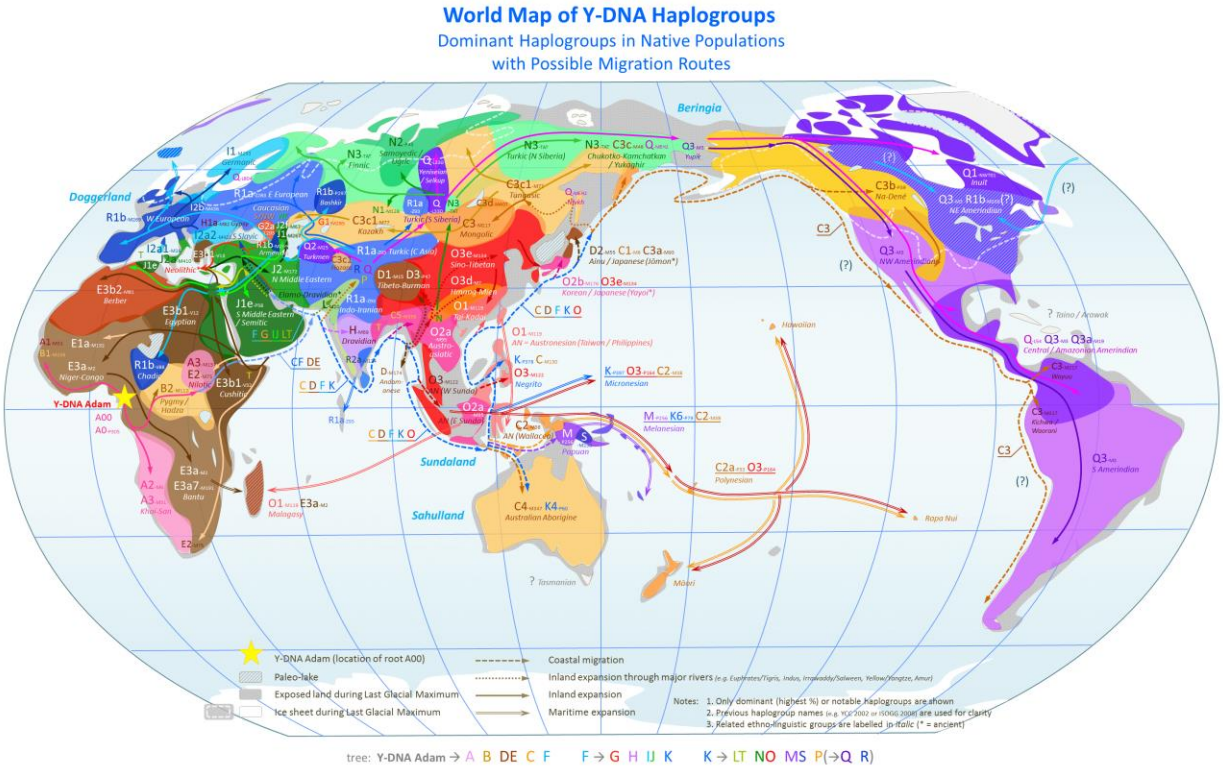

Figure 2.5. The dispersal of Y chromosomal haplogroups. Image under a Creative Commons License: https://creativecommons.org/licenses/by-sa/3.0/. Url: https://commons.wikimedia.org/wiki/File:World_Map_of_Y-DNA_Haplogroups.png

The worldwide distribution of Y haplogroups, as with mtDNA haplogroups, allow for identification of paternal continental origins. Haplogroup E1b1 is found throughout the African continent, with a lower frequency of haplogroups A and B (Arredi, et al., 2004). In Europe, the Y- diversity largely represents five major haplogroups: R, I, J, G, and E. The most common haplogroup, R1b is associated with the expansion out of the Iberian Peninsula following the Last Glacial Maximum (Capelli, et al., 2003; Roewer, et al., 2005; Semino et al., 1996). In the Americas, most of the native Y lineages belong to haplogroup Q found at a frequency of 75 percent in all native populations (Zegura, Karafet, Zhivotovsky, & Hammer, 2004).

Over the last 10 years, technological advances have led to a decreased cost and time investment when examining autosomal markers, which allow for a more complete investigation of a population's history. Halder et al. (2008), developed a panel of a few hundred ancestry informative markers. Just under ten years later, arrays have been developed to examine hundreds of thousands of autosomal single nucleotide polymorphisms throughout the entire genome. However, these large scale whole genome methods have not been applied towards understanding the genetic history of the Garifuna.

On the Islands of St. Vincent

During the war on St. Vincent, the British were actively moving Caribs with African features to the island of Baliceaux, while returning any "Yellow" Caribs amongst the prisoners back to St. Vincent. However, it was not long after the deportation had concluded that the British realized some Black Caribs had remained hidden in the forested areas of the island. Evidence began to emerge that Island Caribs were still in communication with the Black Caribs that had eluded capture. Eventually, the capture of a Black Carib chief and about nine of his

followers, confirmed these reports (Talyor, 2012). In 1805, Britain pardoned the remaining Black Caribs and granted them land at Morne Ronde. Some forty-five Black Caribs, the families of two brothers consisting of sixteen men, nine women, and twenty children, surrendered to Morne Ronde (Talyor, 2012; Gullick, 1984).

In 1806, a group of 105 Caribs established a settlement in Great Sandy Bay at Owia, a community that remains the largest Carib settlement in St. Vincent (Talyor, 2012). After a volcanic eruption hit Morne Ronde in 1812, some 120 Island Caribs (mostly "Yellow" Caribs), asked to be moved to Trinidad, while many of the Black Caribs remained behind (Talyor, 2012). For the next several decades, the "Yellow" and "Black" Caribs generally occupied different communities, but following emancipation contact between the populations increased, and admixture became more common (Gullick, 1984).

Figure 2.6. Map of St. Vincent with sites included in this study (Fancy, Owia, Sandy Bay, and Greiggs), as well as Kingstown where the majority of samples were collected by Benn Torres et al. (2015).

In the years that followed, a series of events altered the biological makeup of the St. Vincent Caribs. Waves of epidemics hit the island including a smallpox epidemic in 1849 and a cholera epidemic in 1860 that killed around 2000 Caribs (Gullick, 1984). A devastating hurricane hit in 1898, leading to about 300 deaths on the island. And, in 1902, another volcanic eruption led to the displacement and resettlement of the survivors. Most of these movements were within the island of St. Vincent. However, during WWII, labor opportunities in the oil industries of Aruba and Trinidad began external movements (Gullick, 1984).

Biological investigations on St. Vincent Garifuna reflect these historical events. Some of the earliest research, which began in the mid-1970s, relied on anthropometrics, blood and immunoglobulin polymorphisms. By this time, the large majority of the population on St. Vincent displayed African phenotypes. Despite this, St. Vincent had lower frequencies of African classical markers, particularly a *rhesus* haplotype that is common in African populations, compared to other Afro-Caribbean groups. Admixture estimates using blood polymorphisms indicated a 44 percent Native American contribution (Crawford, Dykes, Skradsky, & Polesky, 1984; Schanfield, Brown, & Crawford, 1984; Devor, Crawford, & Bach-Enciso, 1984). These studies showed that the St. Vincent Garifuna had the highest frequency of Native markers when compared to Creole groups on the island, as well as other African groups, including Garifuna, on the mainland. Anthropometrics have also been used to show the uniqueness of the St. Vincent Garifuna. A study by Lin (1984) compared the Garifuna of St. Vincent to those found in Guatemala. He concluded that differences in body shape and size, where the males of St. Vincent tended to be bulkier than those found on the coast, were due to the combined effects of 180 years of separation, differences in admixture, as well as differences in environment. Given

the purge of Caribs with African phenotypes during the late 1700s, these difference displayed by St. Vincent Caribs when compared to other Garifuna were not surprising.

Over the last ten years, molecular methods have been used to examine the genetic makeup of the Garifuna and other groups on the island of St. Vincent. The first molecular study on St. Vincent examined English speaking Afro-Caribbean groups, largely from Kingstown on the southern coast of St. Vincent (Benn Torres, Kittles, & Stone, 2007). In this sample, only one individual carried a mtDNA haplotype common to the Americas, belonging to haplogroup A (Figure 2.7). Over 90 percent of the Creole participants carried African lineages belonging to the superhaplogroup L (Benn Torres, Kittles, & Stone, 2007). Another study of mitochondrial DNA by Benn Torres et al. (2015) focused on St. Vincent Garifuna, largely from Kingstown. Similar to the English speaking group in the previous study, most lineages belonged to African L haplogroups. However, about 16% of the individuals carried the Native American A2 haplogroup, and another 21% belonged to haplogroup C1, with little diversity seen within these haplogroups. Another study focused largely on the northern Garifuna communities of Sandy Bay, Owia, and Fancy, as well as a southern community at Greiggs (Phillips-Krawczak, 2012). The northern communities have a slightly higher frequency of A and C haplotypes at 44%. African L haplogroups were common here as well, and a small contribution of other haplogroups, including an individual with a European haplotype, were also detected. These studies show that historical factors have shaped the genetic landscape of St. Vincent, with a high frequency of Amerind markers when compared with other African admixed groups throughout the Caribbean.

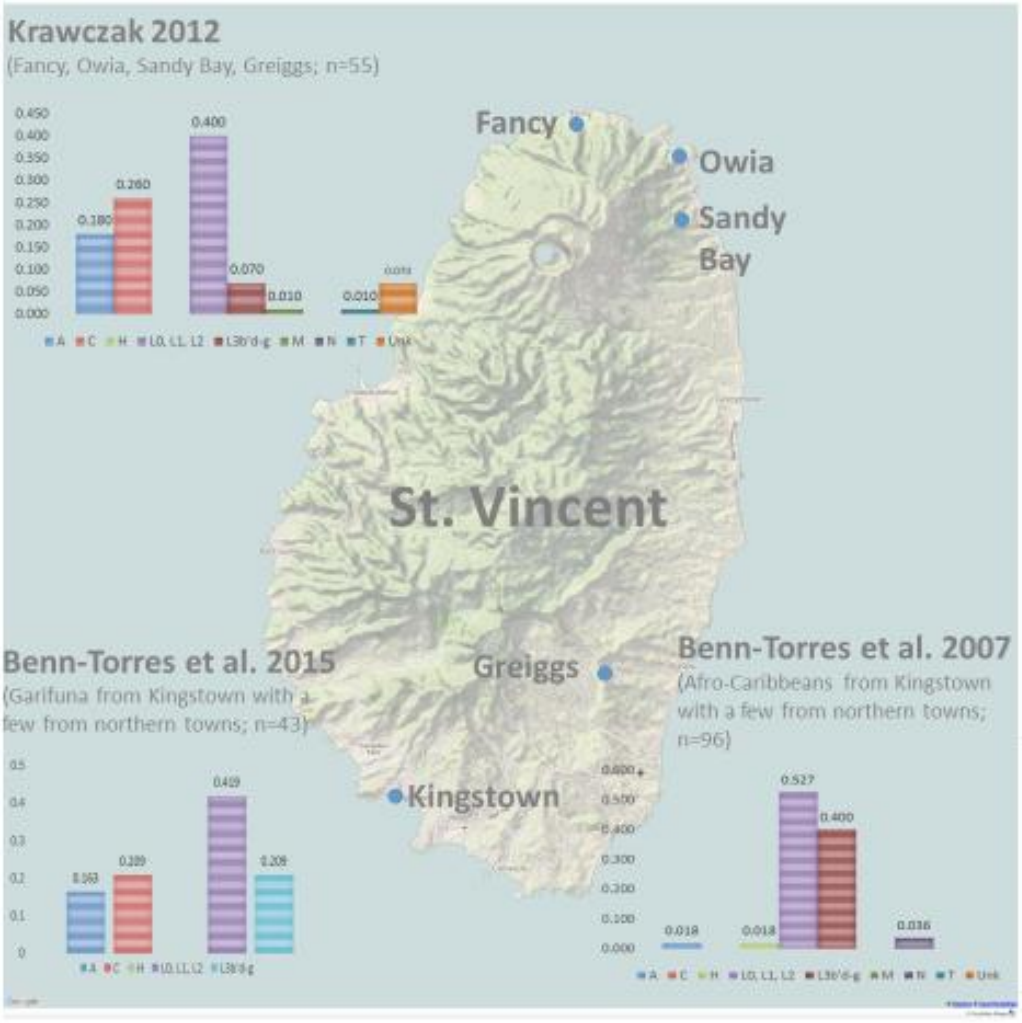

Figure 2.7. MtDNA haplogroups found on St. Vincent from previous studies (Benn Torres, Kittles, & Stone, 2007; Phillips-Krawczak, 2012; Benn Torres, et al., 2015).

Y chromosome variation in St. Vincent Garifuna was also examined by Benn Torres et al. (2015), using a combination of single nucleotide polymorphisms (SNPs) and short tandem repeats (STRs). Of the 30 haplotypes found on St. Vincent, 15 belonged to African haplogroup E1b1a, 11 belonged to European haplogroups I and R, and 4 were found that belonged to the Native American haplogroup Q1a3 (Figure 2.8). The Q1a3 haplotypes more closely resemble

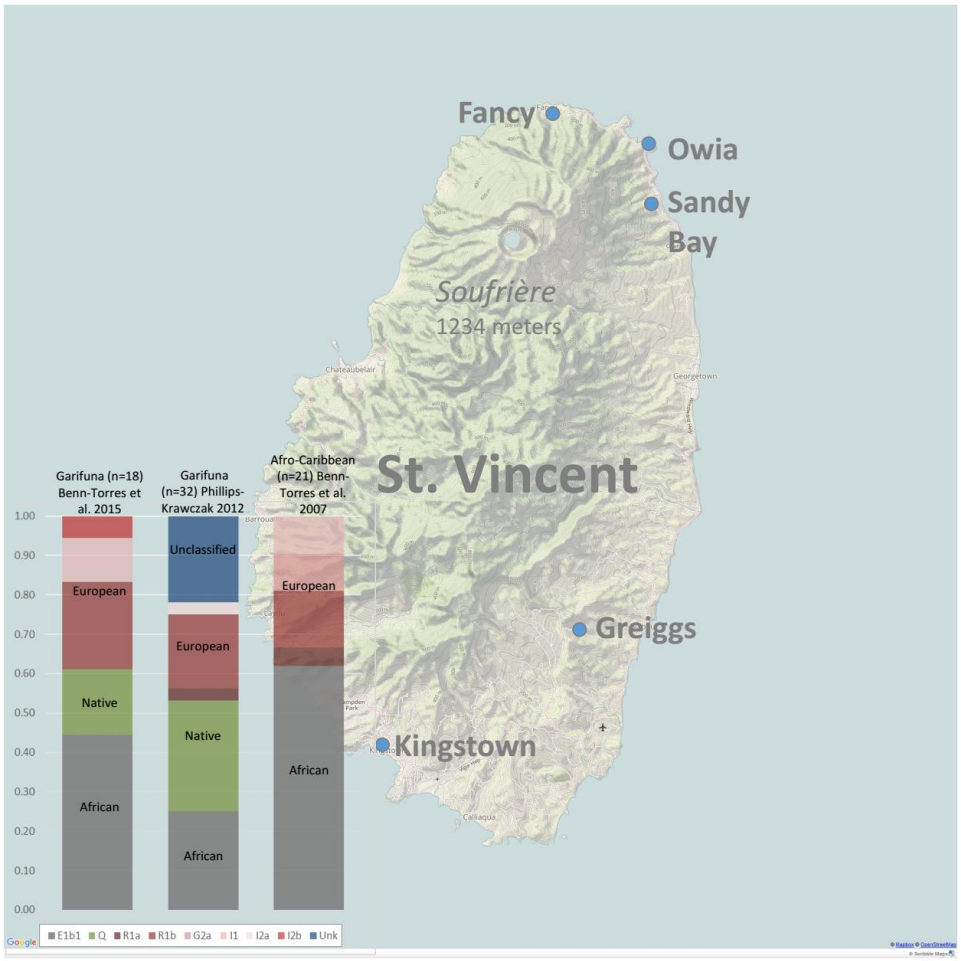

Figure 2.8. Y haplogroup frequencies from three studies on the island of St. Vincent. Y haplogroups were inferred for the Garifuna sample from Phillips-Krawczak (2012) and Benn-Torres et al. (2007) using Whit Athey's Haplogroup predictor. African haplogroup E1b1 is shown in gray, Amerind haplogroup Q is shown in green, European haplogroups are shown in reds, and unclassified haplotypes are shown in dark blue (Benn Torres, et al., 2015; Phillips-Krawczak, 2012; Benn Torres, Kittles, & Stone, 2007).

those found in South America rather than haplotypes found in Central America. These data show that, as with many admixed populations, male admixture rates can differ from females. In this St. Vincent sample, roughly 13 percent of the males have a Q haplotype, and there is a strong European contribution to the paternal gene pool (Benn Torres, et al., 2015). St. Vincent Garifuna were also studied by Phillips-Krawzack (2012), including 32 males from Fancy, Owia,

Sandy Bay and Greiggs. This sample, collected largely from the northern part of the island where Garifuna were historically present, had a higher frequency of Q haplotypes (28%). African haplotypes represented 25 percent of the sample, and European haplotypes made up 25 percent of the classified samples. A further 22 percent of the sample could not be assigned to a haplogroup without more information.

On the Island of Dominica

After the Carib reserve was created on the Island of Dominica in 1903, it continued to be a haven for the original peoples of the Caribbean. Some individuals began to move there from St. Vincent, although only 9 were recorded as having been born on St. Vincent in the 1921 census of Dominica (Gullick, 1984). The Kalinago Reserve, as it is called today, contains the largest Native Caribbean community found in the Lesser Antilles (Benn-Torres, Stone, & Kittles, 2013). The people of the island do not refer to themselves as Garifuna, but instead use the name Kalinago in reference to origin stories of the Kalina, who were thought to have migrated into the Lesser Antilles from South America long before European arrival (Davis & Goodwin, 1990). As the Kalinago exhibit phenotypic features indicating admixture with African and European groups, they have also been of interest to biological researchers interested in the origins of Garifuna and other Afro-Caribbean groups.

Molecular studies of mtDNA in Dominica began in 2007, when a group of self-described African-Caribbeans were sampled by Benn Torres et al., (2007). The study found that the majority of individuals had a mitochondrial haplogroup of African origin, with L haplogroups being the most common (Figure 2.9). In Dominica, 28 percent of the lineages were of Native American origin, with a low gene diversity indicative of a small founding population, and a high

nucleotide diversity indicated a high level of admixture (Benn Torres, Kittles, & Stone, 2007). Another study by Phillips-Krawczak (2012), sampled individuals from Dominica that identified as Caribs, from the Kalinago Reserve. This study found a higher Native American contribution (58%), largely through haplogroup C (50%), of maternal ancestry and illustrates how local factors can influence the genetic structure of groups in small geographic space.

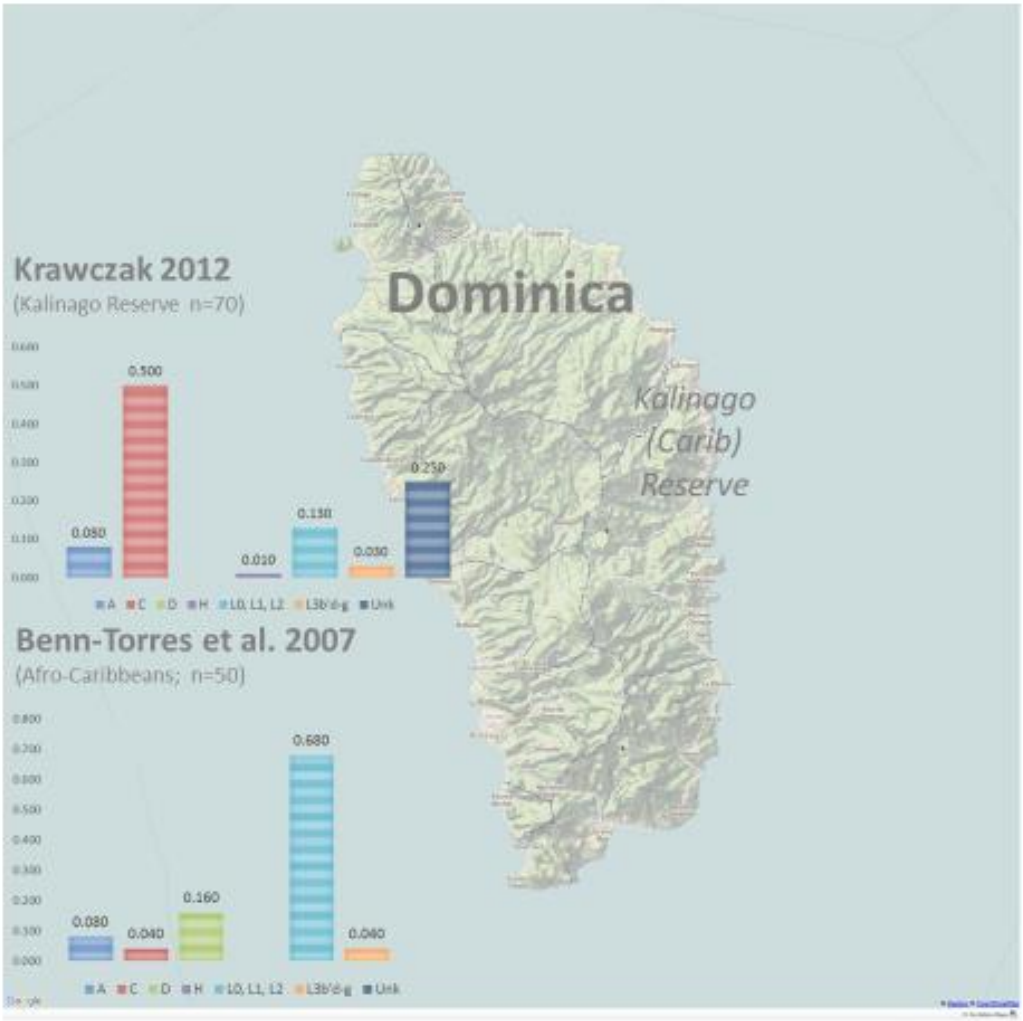

Figure 2.9. MtDNA haplogroups in previous studies on the island of Dominica (Phillips-Krawczak, 2012; Benn Torres, Kittles, & Stone, 2007).

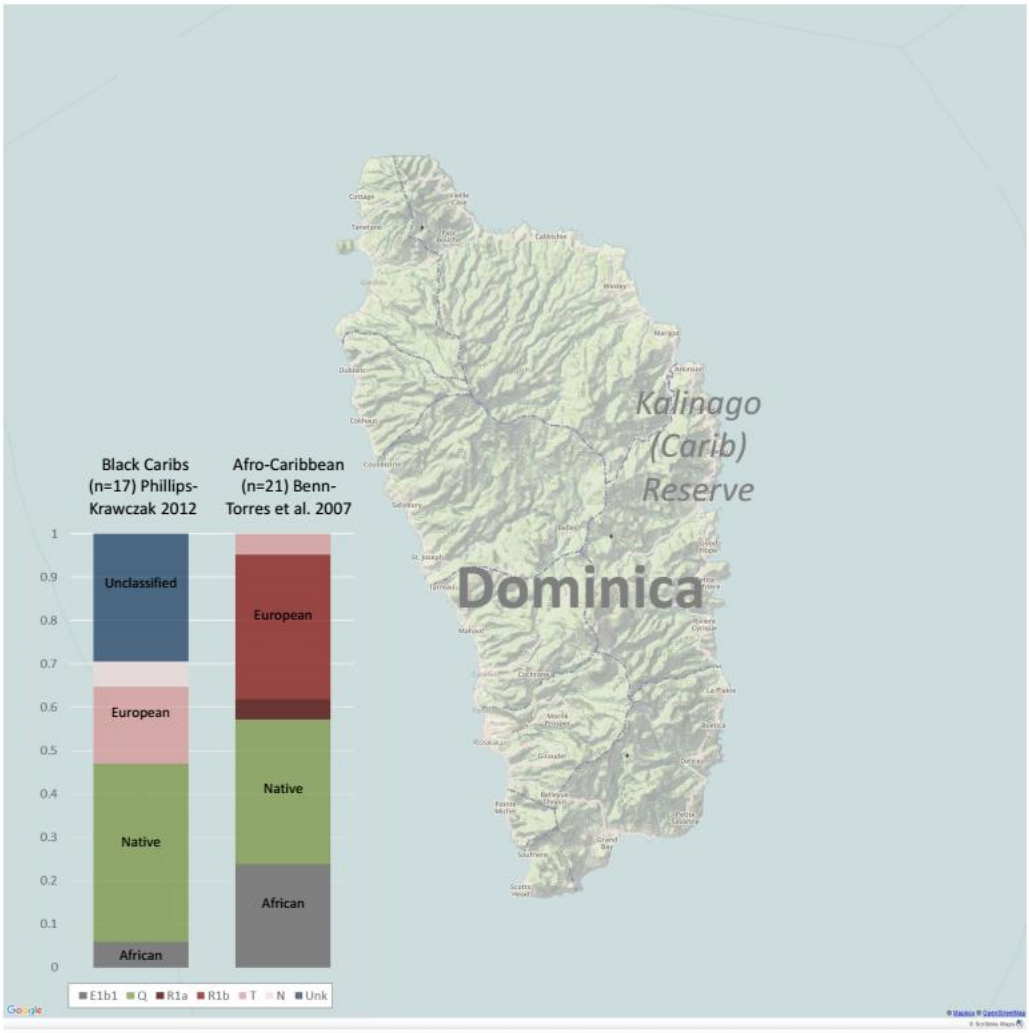

Figure 2.10. Estimates of inferred Y haplogroups using Whit Athey's Haplogroup predictor for two Dominica samples. African haplogroup E1b1 is shown in gray, Amerind haplogroup Q is shown in green, European haplogroups are shown in reds, and unclassified haplotypes are shown in dark blue (Phillips-Krawczak, 2012; Benn Torres, Kittles, & Stone, 2007)

The Y chromosome was also examined on the island of Dominica. Benn Torres et al. (2007), sampled English speaking individuals of African descent and found a low African contribution to the paternal gene pool at 34.1%, lower than that seen in other Afro-Caribbean communities in the Caribbean (Figure 2.10). Phillips-Krawczak (2012) found an even lower

contribution in participants from the Kalinago reserve, although nearly 30% of the sample was not assigned to a particular haplogroup. Haplogroup Q was identified at a high frequency in both samples, with a frequency of 41.2 percent in the Reserve (Phillips-Krawczak, 2012) and 33% in the group studied by Benn Torres et al. (2007). Additionally, a large European contribution was seen in each sample between 23.5-43%.

On the Island of Roátan

The island of Roátan is located off the northern coast of Honduras, the largest of the Bay Islands roughly 60 km long and 5 km wide. It is part the Mesoamerican Barrier Reef. The island has become a tourist destination, with cruise ports and resorts targeting those interested in exploring Roátan's marine life. Most of the communities and people on Roátan are made up of Creoles who retain English names and speak English as their first language, a remnant of British occupation that persisted until 1860 (Kirtsoglou & Theodossopoulos, 2004).

Roátan was first settled by Garifuna in April of 1797, but at the time of settlement most Garifuna found it poor ground for farming, and by October of 1797, only 206 Black Caribs remained on the island (Talyor, 2012). Upon arrival, all Garifuna surnames that were given were of French origin, if they were provided at all (Gonzalez N. L., 1984). However, the majority of surnames found today are of Spanish origin. Today, most of the 2000 Garifuna inhabitants of the Bay Island are located in Punta Gorda, a small town on the northern coast of the island (Richards, 2003).

The first biological study of the Garifuna in Roátan examined dermal prints of individuals and compared them to Black Carib and Creole groups in Guatemala, Belize and the Honduran coast. The results showed that the individuals on Punta Gorda, particularly female

participants, showed a distinct dermal pattern, which may be the result of differential mobility between the sexes (Lin, et al., 1984).

Classical markers have also been used to examine the origins of Garifuna on the island of Roátan. Abnormal hemoglobins were examined by Custodio & Huntsman (1984) to compare rates of the sickle-cell trait in Garifuna against those of other Afro-Caribbean groups. The study found a sickle cell carrier rate of 13.1% in Punta Gorda, intermediate to those found on the Honduran and Belizean coast (Custodio & Huntsman, 1984). Blood group polymorphisms were also examined by Custodio et al. (1984). This study showed evidence of admixture between island groups and the West Africans brought to the region through the slave trade, with Garifuna from Roátan, as well as other Garifuna from Belize and Honduras, having blood group polymorphisms frequencies somewhere intermediate between Native American and African source populations (Custodio, et al., 1984).

On the Honduran Coast

Upon arrival in Trujillo, the Garifuna establised the two communities of Rio Negro and Cristales (Herrera-Paz E. F., 2017). The survivors of St. Vincent were not the only peoples of mixed African ancestry that established settlements during this time. Around 300 French speaking ex-slaves, from Haiti and other French islands in the Caribbean, worked as mercenary soldies for the Spanish in Truijillo (Gonzalez N. L., 1984). Other Creole groups were working in Spanish mines, and would later work in the fruit plantations that eventually emerged throughout Central America (Crawford M. H., 1984). Miskito Indians, a hybrid Indian and African group, had lived along the coast of Central America since the 17th century, after a group of slaves successfully revolted on a ship and were welcomed by the inhabitants of the region (Gonzalez N.

L., 1984). While cultural evidence of admixture between these groups is scarse, the rapid population growth of the Garifuna during the 19th century was, in part, the result of gene flow from other Afro-Caribbean groups into Garifuna villages (Crawford M. H., 1984).

Shortly after arriving in Trujillo in 1797, Black Caribs quickly spread along the coast in search of good fishing grounds, farmable land, and places where they could aquire wage labor (Herrera-Paz et al., 2010; Talyor, 2012). This early movement was typically accomplished by the migration of entire families, who would eventually make up the founders of new villages that arose along the coast throughout the 19th century (Herrera-Paz, et al., 2010). This migration was rapid, and by 1802 some of the first settlements begain to appear in current day Belize (Firschein, 1961). As slavery was abolished in the region during the 19th century, the demand for Garifuna labor increased in areas of agriculture, mahogany trade, carpentry and turtle fishing (Talyor, 2012; Anderson, 1997). By the mid-1800s, Garifuna villages occupied 400 miles of the Central American coast, stretching through Nicaragua, Honduras, Guatemala, Belize, as well as on Roátan (Firschein, 1961).

Early research on the Honduran coast began in the 1970s, with dermatoglyphics and classical blood polymorphisms examined (Lin, et al., 1984; Custodio & Huntsman, 1984; Custodio, et al., 1984). These studies supported the idea of admixture, largely between West African and Native American populations and found a lower diversity when compared to populations on St. Vincent, suggesting that both founder effect and natural selection differentiated the Garifuna villages. The first molecular work was published by Salas et al. (2005), examing the mitocondrial DNA of 44 Garifuna from the Honduran coast. The study found that roughly 84 percent of the lineages were of African origin, and the reduced diversity in these sequences were consistent with a population that had undergone a series of bottlenecks.

Thirteen autosomal STRs and isonymy, using surnames as an indicator of paternal ancestry, were used to examine the villages of Bajamar, Iriona, and Corozal on the Honduran coast (Herrera-Paz, Matamoros, & Carracedo, 2010). The study showed that there has been an increase in migration over the last few generations, with a shift from neolocality to matrilocality. This shift could have implications on the genetic makeup of the population, reducing the diversity of mtDNA variation in a villages, while increasing the diversity seen in the Y chromosome. Later work by Salazar-Flores et al., (2015) using data from (Herrera-Paz, Matamoros, & Carracedo, 2010), in the communities of Bajamar, Iriona and Corozal to compare them to other groups in the Caribbean and Central and South America. These 3 communities have more African contributions to their gene pool than any other groups in the region, with two distinct waves of migration: one from the earliest slave ports on the Western Coast, and a second wave found originating with later movements that included slaves from Southern Africa. As with previous studies, the Garifuna from these villages have a mostly African genome, with some Native American and European contributions.

Summary of Previous Biological Investigations

Overall, previous research indicates that the Garifuna of Central America are an admixed population consisting of African, Native American, and some European DNA. The Kalinago of Dominica and the Garifuna of St. Vincent tend to be more genetically diverse, and have higher rates of Native American contributions, particularly from the maternal side, when compared to other Afro-Caribbean groups. Garifuna on the coast tend to have a higher rate of African markers, with more isolated communities exhibiting decreased levels of genetic diversity.

Chapter 3: Materials and Methods

Samples were collected from some of the earliest sites of Garifuna settlement including Punta Gorda on the island of Roátan, Cristales and Rio Negro in Trujillo, and Santa Fe on the Honduran Coast. In order to examine the paternal and maternal histories of these groups, demographic data, mtDNA, and Y chromosome data were collected for each site. The following chapter describes the data collected, and the laboratory and statistical methods used to address questions of Garifuna origin, and the effects of drift, admixture and migration.

DNA and demographic information collected

In collaboration with Dr. Norberto Baldi, from the Universidad de Costa Rica, and Dr. Edwin Herrera from the Universidad Católica de Honduras, DNA samples and demographic information were collected from several communities of Garifuna in Honduras, during January and July of 2014. Approximately 300 individuals participated with informed consent from communities of Trujillo (Cristales and Rio Negro) and Santa Fe on the Honduran coast, and Punta Gorda on the island Roátan (Table 3.1). Demographic questionnaires in Spanish were filled out and included information on participant's place of birth, residence, their parent's and grandparent's place of birth, siblings, ethnic affiliation, language(s), occupation, education, number of children, household composition, and migration history. DNA samples were collected via buccal swabs and blood spots on FTA cards or Whatman filter papers in all communities. Mouth rinses of 10 mL distilled H_20 were also collected in the three coastal barrios of Rio Negro, Cristales, and Santa Fe. This project was reviewed by the Internal Review Board at the University of Kansas (HSCL #16735).

Table 3.1. Materials collected that were included in this study.

Samples	Island/Country	Village	n
Previous collections	St. Vincent Christine Phillips-Krawzack Spring 2004	Fancy	24
		Sandy Bay	34
		Owia	22
		Greggs	20
	Belize, CPK Winter 2005	Punta Gorda	50
		Barranco	27
	Dominica, Dr. Crawford 2005	Kalinago Reserve	70
Fieldwork	Honduran Coast January 2014	Cristales	44
		Rio Negro	76
		Santa Fe	60
	Roatan, July 2014	Punta Gorda	132
Additional Y-STR data	Honduran Coast Dr. Matamoros	Iriona	7
		Bajamar	26
		Corozal	20

Previous research in the Caribbean provided samples for Garifuna in St. Vincent (4 villages), Dominica, and Belize (2 villages). In 2004, blood samples, blood spots, and demographic information were collected from the Saint Vincent communities of Fancy, Owia, Sandy Bay and Greiggs. Two field trips in 2005 gathered demographic information and blood samples from Belize (Punta Gorda and Barranco villages). In addition, Y-STR data for 11 markers from three villages on the Honduran coast (Corozal, Bajamar, and Iriona) were contributed by Dr. Edwin Herrera, Unidiversidad Católica de Honduras, and Dr. Matamoros, Director of Forensic Medicine at the Public Ministry of Honduras (Table 3.1).

Laboratory methods

DNA was extracted from buccal swabs and mouth rinses using Qiagen QIAamp DNA mini kits, following the manufacturer's instructions (Qiagen, Valencia, California). Samples from individuals that self-identified as Garifuna were then prepared for sequencing of mtDNA hypervariable regions I and II (HVS-I & II), as well as haplogroup defining sequences for restriction fragment length polymorphisms (RFLP) analyses. Samples from Belize, Dominica (Kalinago) and St. Vincent were re-sequenced at mtDNA HVS I, to lengthen the original sequence for better comparison with more recent data, and sequenced for HVS-II. Polymerase chain reactions (PCR) were performed using 5.0 µl of 5x GoTaq Flexi buffer, 4.0 µl of $MgCl_2$, 1.0 µl of BSA, 0.4 µl of GoTaq Polymerase, 0.5 µl of dNTPs, 7.1 µl of ddH_2O, and 1 µl of the forward and reverse primers shown in Table 3.2, and 2 µl of DNA at roughly 1 ng/µl concentrations. Reactions were run under the thermocycler profile shown in Figure 3.1, and visualized using UV electrophoresis. PCR products were sent to Beckman and Coulter Genomics (now Genewiz) for Sanger sequencing of the mitochondrial DNA hypervariable regions I and II.

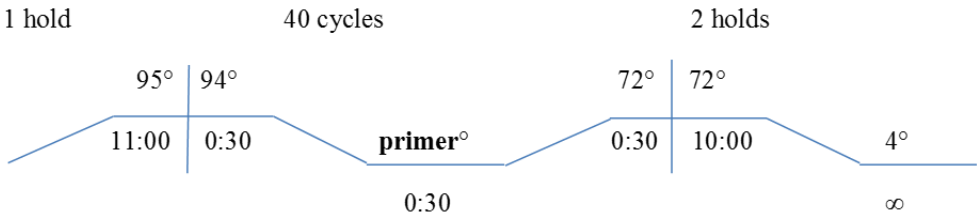

Figure 3.1. Thermocycler profile for mtDNA PCR reactions.

Table 2.2. Primers, annealing temperatures, and restriction enzymes used in this study.

Haplogroup/ Region	Primer	Sequence 5' - 3'	Annealing Temperature	Restriction Site
HVS-I	L15879	AAT GGG CCT GTC CTT GTA GT	56	na
	H16459	GCT ACC CCC AAG TGT TAT GG		
HVS-II	L16544	GAG CTC TCC ATG CAT TTG GT	57	na
	H00500	GCG GGG GTT GTA TTG ATG AGA		
L0-L2	L3388	CTA GGC TAT ATA CCA CTA CGC	47	+3592 HpaI
	H3745	CTA GGG TGA CTT CAT ATG AG		
A	L534	CCC CAT ACC CCG ACC CCG AAC CAA CC	58	+663 HaeIIII
	H725	CGT GAA CTC ACT GGA AGG GG		
C	L13001	GCA AAT CAG CCC AAT TAG GT	53	-13259 HincII/
	H13403	ATA TCT TGT TCA TTG TTA AGG TTG		+13262 AluI
B	L8144	ACC GGG GGT ATA CTA CGGT	54	9 bp deletion
	H8366	TTT CAC TGT AAA GAG GTG TTG G		np8281-8289

Restriction fragment length polymorphisms were performed in a hierarchical method to identify samples belonging to haplogroups L0-L2, L3d, C, and A, and analyses were performed using the primers and enzymes shown in Table 3.3 Restriction digest was performed using 9.0 µL of sterile water, 1.0 µL of BSA, 2.0 µL of an enzyme specific buffer, and 0.5 µL of the restriction enzyme, and 7.5 µL of PCR product. Samples were incubated for approximately 12 hours at 37°C, and results were visualized on a 3% NuSieve 3:1 agarose gel stained with ethidium bromide under a UV fluorescent light. Haplogroup B was tested by amplifying the region of a 9 base pair deletion that characterizes the haplogroup, and running the PCR products on a 3% NuSieve 3:1 gel and visualizing in UV fluorescent light.

Blood spots from self-identified Garifuna males in the three coastal villages of Cristales, Rio Negro, and Santa Fe were sent to Dr. Reena Roy, of Penn State, for Y-STR analysis using a Yfiler Plus kit (Thermo Fisher Scientific). Twenty-seven loci were examined including DYS19, DYS385a/b, DYS389I/II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439,

DYS448, DYS456, DYS458, DYS635 (Y GATA C4) and GATA H4, DYS460, DYS481, DYS533, DYF387S1 a/b, DYS449, DYS518, DYS570, and DYS627 (information included in Table 3.3).

Comparative data

Comparative data have been pooled from the literature to include African populations that represent regions where African slaves were taken and brought to the Americas (including Senegambia, the Windward and Gold Coasts, Bight of Benin, Bight of Biafra, West Central Africa, Southeastern Africa and Madagascar), contemporary Afro-Caribbean groups, European groups most active in colonization of the Caribbean, as well as groups from Central and South America. Sources used in these analyses are found in Appendix A.

Statistical methods: mtDNA

MtDNA sequences for the hypervariable regions I and II were aligned using CLUSTAL in MEGA 6.06 (http://www.megasoftware.net/) (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013) against the revised Cambridge Reference Sequence (rCRS) (Andrews, et al., 1999). Summary statistics of mtDNA sequences included: Nei's gene diversity statistic (H) (Nei, 1987), Tajima's (1993) mean number of pairwise differences between haplotypes within a sample (π), and estimates of the expected diversity in a population (θ). Garifuna and Black Carib HVS-I and HVS-II sequences were examined between nucleotide positions (nps) 16024-16400 (HVS-I) and nps 80-400 (HVS-II) for diversity measures computed in Arlequin ver. 3.5.1.2 (http://cmpg.unibe.ch/software/arlequin35/) (Excoffier & Lischer, 2010). Gene diversity (H), similar to heterozygosity using diploid data, measures the probability that two randomly selected haplotypes from a sample will be different and is defined as:

$$H = \frac{n}{n-1}(1 - \sum_{i=1}^{k} p^2) \quad (1)$$

where n with number of samples, k is the number of haplotypes, and p_i is the frequency of the i^{th} haplotypes within the sample (Nei, Molecular Evolutionary Genetics, 1987). While gene diversity examines the relationship of whole sequences to one another, the average number of pairwise differences (π) provides information about how similar or different sequences within a sample are, and is defined by the equation:

$$\pi = \frac{n}{n-1}\sum_{i=1}^{k}\sum_{j=1}^{k} p_i p_j d_{ij} \quad (2)$$

where n represents the size of the sample, d_{ij} estimates the number of mutations that differentiate haplotypes i and j, k equals the number of haplotypes within a sample, p_i equals the frequency of each haplotype i (Tajima F. , 1993).

Expected diversity (θ) of a haploid locus equals $2N_e\mu$, where N_e is the effective population size and μ is the mutation rate of the marker studied. Theta can be estimated in a number of ways, including using gene diversity (H), the number of expected alleles (k) in a sample, and the number of segregating sites (S). An estimator of θ based on the expected number of alleles (k) in a population and the sample size in relation to the expected diversity found in the population is computed as θ_k, which equals:

$$\theta_k = \theta \sum_{i=0}^{n-1} \frac{1}{\theta + i} \quad (3)$$

(Ewens, 1972). A 95 percent confidence interval around θ_k is computed by assessing the probability that k will equal 0 (lower bound) and 1 (upper bound), and are the sums of the

probability of observing *k'* alleles when *k'*=0,…*k* (Excoffier & Schneider, 2005). Theta *S* estimates the expected diversity within a population using the number of segregating sites in a sample, and is defined by the equation:

$$\theta_S = S / \sum_{i=1}^{n-1} \frac{1}{i} \quad (4)$$

where *S* is the number of segregating sites (Watterson, 1975). Measurements of mtDNA sequence diversity use the infinite sites model, proposed by Kimura (Kimura, 1969), which assumes that when the mutation rate at each site is small and the number of sites in a DNA segment is large, the probability that a mutation will occur more than once at the same site is negligible. Measures of expected diversity were computed in Arlequin 3.5.1.2 and plotted in R version 3.3.3 (https://www.r-project.org/).

Tajima's *D* and Fu's *Fs*, two measures of neutrality, were also computed on sequence data in Arlequin 3.5. Both methods depend on the infinite-sites model that assumes no recombination. Tajima's *D* compares θ_π, which is equal to π as defined by Equation 2, and θ_S by randomly generating samples under a hypothesis of selective neutrality in a population that is in equilibrium. Tajima's *D* is defined by the following equation:

$$D = \frac{\theta_\pi - \theta_S}{\sqrt{Var(\theta_\pi - \theta_S)}} \quad (5)$$

(Tajima F. , 1993). A significant *D* value can indicate a population under selection, e ın, or contraction (Excoffier & Schneider, 2005). Fu's F_S statistic tests neutrality by randomly generating samples from the pool, and is defined by the equation:

$$F_S = \ln(\frac{S}{1-S}) \quad (6)$$

where *S* represents the probability that randomly generated values of *k* (*K*) will be greater or equal to the observed values of *k*, so that θ equals θ_π. The F_S statistic is particularly sensitive to demographic expansions, which will yield large, negative values with p-values of 0.02 and below (Fu, 1997; Excoffier & Schneider, 2005).

Molecular diversity in a population can also be examined through mismatch distributions, which can provide evidence of demographic events in a population's history. If a distribution has a unimodal distribution, it may represent a recent expansion event; a multimodal distribution can indicate a population that has maintained a constant size over time (Rogers & Harpending, 1992). Computations of mismatch distributions were undergone using a finite-sites model that recognizes differences in mutations rates, which better takes into account mtDNA variability (Schneider & Excoffier, 1999). A raggedness index (*r*) can assess the fit of a mismatch distributions, as a higher index is found in a static population that usually produces a multimodal distribution (Harpending, et al., 1993). This index is calculated using the following equation:

$$r = \sum_{i=1}^{d+1} (x_i - x_{i-1})^2 \qquad (7)$$

where *d* is the maximum differences between haplotypes, and *x* is the relative frequency of the mismatch within all mismatches in the population. Mismatch distributions were calculated in the Kalinago and Garifuna populations included in this study and available in the literature using Arlequin v. 3.5.1.2 and graphs were produced in R version 3.3.3 (https://www.r-project.org/).

Intrapopulation measures were also calculated in Arlequin v. 3.5.1.2 and graphs were R version 3.3.3. Measures included Nei's average number of difference between populations (D_A),which is expected to equal:

(8)

$$D_A = 2\mu\tau$$

where μ equals the average mutation rate, and τ represents the divergence time between two populations (Nei & Li, 1979) . Reynold's coancestry coefficient was also computed as:

$$F_{ST} = 1 - \left(1 - \frac{1}{N}\right)^t \approx 1 - e^{-1t/N}, \quad (9)$$

where, *N* is the size the population and *t* is the number of generations that the two populations have diverged (Reynolds, Weir, & Cockerham, 1983).

Median joining (MJ) networks were computed for Garifuna and Black Carib mtDNA haplotypes that belonged to major African haplogroups L0, L1, L2, and L3, and Amerindian haplogroups A2 and C1 in Network 5.0.0.1 (http://www.fluxus-engineering.com/sharenet.htm). MJ networks are used to examine the relationships between haplotypes, and can infer ancestral haplotypes that are no longer found within a population. Because mutation rates differ at various sites (Sores, et al., 2009), a weighting system was used that weighted mutations that occur at a high frequency to 1 (nps 146, 150, 152, 195, 16093, 16129, 16189, 16311, 16362), positions where mutations occur at a moderate frequency to 2 (204, 207, 16172, 16192, 16223, 16278, 16291, 16319), and all other mutations in HVS-I and II were weighted at 4.

Multidimensional Scaling (MDS) was used to visualize the relationship of different populations in this study using a two dimensional plot. A traditional MDS analysis was constructed using Tamura & Nei's (1993) distances for mtDNA sequence data, as it accounts for differences in transversion and transition rates, as well as transition rates between purines or pyrimidines (Excoffier & Schneider, 2005). Distance matrices were calculated in Arlequin

3.53.5.1.2, and the plots were constructed in R version 3.3.3, and then edited manually. MDS plots were constructed to examine: 1) the relationship between Kalinago and 8 Garifuna communities; 2) Garifuna villages in relationship to Caribbean, Central American, South American, and African groups; and 3) to examine the relationship of the St. Vincent samples and Honduran coastal populations as a group in relation to other comparative samples.

Analysis of molecular variance (AMOVA) was performed in Arlequin 3.5.1.2, using two separate groupings (Excoffier, Smouse, & Quattro, 1992). AMOVA was first calculated using only the Garifuna and Kalinago populations using the following groupings: Lesser Antilles (Dominica and St. Vincent), Punta Gorda, Honduran Coast (including Cristales, Rio Negro, and Santa Fe), and Belize. A second AMOVA was computed with the above groupings and, additionally Free Peoples of Trinidad, admixed groups from Central America (Mestizos from Nicaragua and Maya from Mexico), Arawak and Cariban Speakers from Panama and Peru, African admixed populations (Choco of Columbia and Nori Marron of French Guiana), African populations.

Statistical methods: Y Short Tandem Repeats

Y haplogroup assignments, following the Y Chromosome Consortiums nomenclature, were inferred using a Bayesian allele frequency approach using all Y-STR loci except DYS518, DYS627, and DYF387S1 (http://www.hprg.com/hapest5/) (Athey, 2006). The haplogroup predictor was set to [Equal Priors] in the Area selection drop down menu. Haplogroup assignments were only given when the probability of assignment was greater than 80 percent. All other haplotypes were assigned as unknown. This method was also used to infer haplogroup assignments for Y-STR data from Corozal, Bajamar, and Iriona, Benn-Torres (2015) and

Phillips-Krawczak (2012), so that haplogroup frequencies from other Garifuna and Afro-Caribbean populations could be compared.

Within population diversity measures were computed for the Garifuna communities of Rio Negro, Cristales, and Santa Fe using all 27 STR haplotypes in Arlequin version 3.5.1.2 (http://cmpg.unibe.ch/software/arlequin35/) (Excoffier & Lischer, 2010). To compute diversity measures within all comparative groups, 10 STR haplotypes (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, and DYS439) were used. Calculations included gene diversity (*H*) (Equation 1), mean number of pairwise difference (π) (Equation 2), and the average diversity of loci (π_n), in Arlequin 3.5 and graphed in R 3.3.3, as described in mtDNA analyses. The average diversity of loci is calculated by:

$$\pi_n = \frac{\sum_{i=1}^{k} \sum_{j<i} p_i p_j d_{ij}}{L} \tag{10}$$

where *L* represents the number of loci. For Y-STR data, the stepwise mutation model was assumed following Ohta and Kimura (1973), which suggests that mutations increases or decreases an allele's length (or a single repeat) with equal probability (Jobling, et al., 2004). Theta estimated from observed homozygosity (θ_H) using microsatellite data, is calculated as:

$$\theta_H = \frac{1}{(1-H)^2} - 1 \tag{11}$$

Intrapopulation measures were computed using all 27 loci to examine the relationship between Cristales, Rio Negro and Santa Fe. These measures included Nei's average number of difference between populations (D_A) and Reynold's coancestry coefficient (Equations 8 and 9), and were calculated in Arlequin 3.3 and graphed in R 3.3.3. These measures were also calculated

for all populations included in these analyses using 10 loci. MDS plots were constructed to visualize the relationship between populations using Slatkin's linearized F_{ST} (Slatkin, 1995). Plots were made to visualize the relationship between 1) 7 Garifuna samples; 2) Garifuna as a group compared to Caribbean, Central American, South American and African populations; 3) 7 Garifuna communities compared to Caribbean, Central and South American groups, African groups, and European populations. In addition, an analysis of genetic relationship using just haplotypes belonging to haplogroup Q was also performed, to visualize the relationship of Q haplotypes found in St. Vincent, the Honduran Coastal communities, and other Caribbean, Central and South American populations. Distance matrices were calculated in Arlequin 3.5, and the plots were constructed in R version 3.3.3, and then edited manually.

Analysis of molecular variance (AMOVA) was performed in Arlequin v 3.5 done using two separate groupings (Excoffier, Smouse, & Quattro, 1992). AMOVA is a way of estimating population differentiation that can parse out the variation that can be explained within a population, within a group of populations, and among groups of populations (Excoffier & Schneider, 2005). The first analysis examined groups by geographic clusters, with the Garifuna left as a separate grouping. Geographic groupings included Caribbean Islands, Central America, South America, Africa and Europe. A second analysis was performed that had the following groupings: admixed groups of largely European and Amerindian admixture (included Mestizos and samples from the general populations of Central and South America), Amerindian groups from the Caribbean, Central and South America (Mayan, Tupi, First Peoples, Arawak and Cariban speakers from South America), Afro-Caribbean populations and Noir Marrons, and populations from Africa.

Median joining networks (Bandelt, Forster, & Rohl, 1999) were created in Network 5.0.0.1, using star contractions to simplify the network (Forster, Torroni, Renfrew, & Rohl, 2001) (http://www.fluxus-engineering.com/sharenet.htm). Y-STRs were weighted based on mutation rates following Wei et al., (2013) (see Table 1). Nodes were constructed in proportion to haplotype frequencies, with the smallest node representing a single haplotype. Networks were created for Y-haplogroup E1b1 and haplogroup Q for the neighborhoods of Cristales, Rio Negro and Santa Fe using 19 Y-STR markers noted in Table 1. Additional Garifuna networks for haplogroups E1b1 and Q were created to include the Garifuna villages of Bajamar, Corozal and Iriona, and used the 10 loci: DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, and DYS439. To determine the relationship of the Y haplotypes and their probable source populations, large networks were created for haplogroups E1b1 and haplogroup Q. For haplogroup E1b1, African populations were included from the Senegambia region, the Windward/Gold Coast, the Bight of Benin, Bight of Biafra, West Central Africa, Southern Africa, and Madagascar, using the 10 loci noted above. To determine the relationship between Garifuna Q haplotypes, networks were created that 1) included all haplotypes that belonged to with haplogroup Q; 2) compared Garifuna with modern Cariban and Arawak speakers from South America; and 3) compared Garifuna with Q haplotypes found in communities that live near Garifuna on the Central American coast (See Appendix A.3.).

Table 3.3. Y-STR markers, their weights used in Network analyses, and their repeat motifs (Wei, Ayub, & Tyler-Smith, 2013; Ballantyne, et al., 2010).

YSTR	Weight	Repeat Motif
DYF387S1	na	(AAAG)3(GTAG)1(GAAG)4N16 (GAAG)9(AAAG)13
DYS19	3	$(TAGA)_3(TAGG)_1(TAGA)_{6-16}$
DYS385a	na	$(AAGG)_4N_{14}(AAAG)_3N_{12}(AAAG)_3\ N_{29}(AAGG)_{6-7}(GAAA)_{7-23}$
DYS385b	na	$(AAGG)_4N_{14}(AAAG)_3N_{12}\ (AAAG)_3\ N_{29}\ (AAGG)_{6-7}(GAAA)_{7-23}$
DYS389I	4	$(TCTG)_3(TCTA)_{6-14}$
DYS389II	3	$(TCTG)_{4-5}(TCTA)_{10-14}N_{28}\ (TCTG)_3\ (TCTA)_{6-14}$
DYS390	2	$(TCTG)_8(TCTA)_{9-4}(TCTG)_1\ (TCTG)_4$
DYS391	5	$(TCTG)_3(TCTA)_{6-15}$
DYS392	3	$(TAT)_{4-20}$
DYS393	5	$(AGAT)_{7-18}$
DYS437	3	$(TCTA)_{4-12}(TCTG)_2(TCTA)_4$
DYS438	4	$(TTTTC)_{7-16}$
DYS439	4	(GATA)3N32$(GATA)_{5-19}$
DYS448	3	$(AGAGAT)_{11-13}N_{42}\ (AGAGAT)_{8-9}$
DYS449	na	$(TTCT)_{13-9}N_{22}(TTCT)_3N_{12}\ (TTCT)_{13-19}$
DYS456	4	$(AGAT)_{11-23}$
DYS458	3	$(GAAA)_{11-24}$
DYS460	na	(TAGA)8-13
DYS481	3	$(CTT)_{22-32}$
DYS518	na	(AAAG)3(GAAG)1(AAAG)14-22 (GGAG)1 (AAAG)4N6 (AAAG)11-19N27(AAGG)4
DYS533	4	$(TATC)_{9-14}$
DYS570	2	$(TTTC)_{14-24}$
DYS576	3	$(AAAG)_{13-22}$
DYS627	na	(AGAA)3N16(AGAG)3 (AAAG)12-24N81 (AAGG)3
DYS635	2	$(TCTA)_4(TGTA)_2(TCTA)_2\ (TGTA)_2\ (TCTA)_2\ (TATG)_{0-2}\ (TCTA)_{4-17}$
YGATA H4	5	$(TAGA)_3N_{12}(TAGG)_3(TAGA)_{8-15}\ N_{22}(TAGA)_4$

*na markers were not included in Network analyses

Genes vs. Geography

Mantel tests were performed to test the relationship between the Nei's genetic distance between populations and geographic distance of each Garifuna village. Genetic distances were calculated in Arlequin 3.5. Geographic distances were computed in R 3.3.3, and the Mantel test was computed using the *ade4* package in R 3.3.3 (Dray et al. 2007). Mantel tests were used to

test the relationship between mtDNA genetic distances and geographic distances, Y-STR genetic distances and geographic distances, as well as mtDNA genetic distances against Y-STR genetic distances.

Table 3.4. Geographic coordinates for locations included in this study.

Location	Lattitude	Longitude
Cristales, Honduras	15.9176	-85.9588
Rio Negro , Honduras	15.9224	-85.9486
Santa Fe, Honduras	15.8977	-86.0319
Bajamar, Honduras	15.8877	-87.8541
Iriona, Honduras	15.9692	-85.0911
Corozal, Honduras	15.7834	-86.6820
Punta Gorda, Roatan	16.4137	-86.3643
St. Vincent, Northern Villages	13.3652	-61.1570
Kingstown, St. Vincent	13.1593	-61.2246
Belize	16.0902	-88.8165
Kalinago Reserve, Dominica	15.5007	-61.2675

Chapter 4: Results

Demographic Information of the Garifuna on the Honduran Coast and Roátan

Demographic information from 292 individuals were collected from participants in Punta Gorda, Roátan, Rio Negro, Cristales and Santa Fe on the Honduran Coast (Table 4.1). Of the participants, 74 percent were female, while 26 percent were male. Thirty-nine percent of the individuals that completed questionnaires were 25 years of age or younger, 32 percent were 46 years of age or older, and individuals between the ages of 26-45 made up 23 percent of the study (Figure 4.1). The mean household size of all Garifuna participants was 4.69 members per household. Women over the age of 40 had an average of 3.77 children, whereas women under the age of 40 had an average of 1.29. All of the participants included self-identified as Garifuna. However, five individuals from Punta Gorda identified as both Garifuna and Ingles, 1 individual identified as Garifuna and Miskito, and another individual identified as Garifuna, Ingles, and Indian. One individual from Trujillo identified as both Garifuna and Creole.

Table 4.1. Demographic information from Questionnaires in 4 Garifuna Villages.

							Age of Individual							
Population	**n**	**M**	**F**	**Mean household size**	**avg # children per woman aged 15-40**	**avg # children per woman over 40**	**<15**	**16-25**	**26-35**	**36-45**	**46-55**	**56-65**	**66-75**	**76-85**
Punta Gorda	119	31	88	5.31	1.59	4.50	22	29	14	7	11	2	3	0
Rio Negro	65	13	52	4.65	1.25	3.67	7	20	9	10	19	3	7	3
Cristales	50	15	35	4.39	1.00	4.27	5	5	4	6	11	13	3	2
Santa Fe	58	18	40	4.42	1.33	2.63	15	10	9	9	3	6	4	2
Total/Average	**292**	**77**	**215**	**4.69**	**1.29**	**3.77**	**49**	**64**	**36**	**32**	**44**	**24**	**17**	**7**

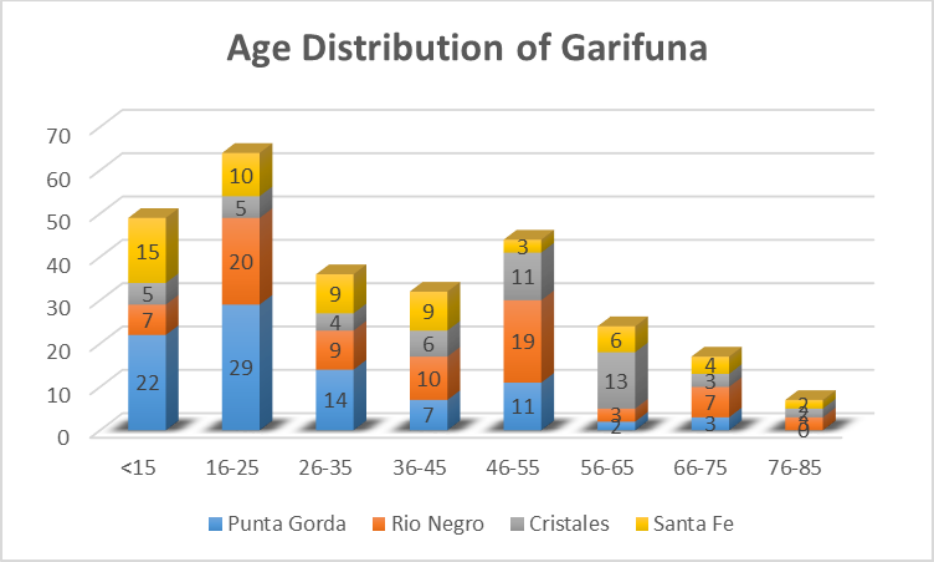

Figure 4.1. Age distribution of Garifuna from 4 villages.

Information on the place of birth of Garifuna participants were also collected and results are shown in Figure 4.2 and Figure 4.3. Eleven of the participants did not reside in the area where the samples were collected, but instead lived in Oak Ridge, on Roátan, or in some of Honduras' larger cities including San Pedro Sula, La Ceiba, El Cerrito and Telgucigalpa. Overall, 68 percent of participants were born in their place of residence, however there were differences seen between the sexes. Seventy-three percent of the women resided in the place of their birth, while only 53 percent of men were born in the place they resided in. This varied by location as well as sex. In Punta Gorda and Trujillo (includes Cristales and Rio Negro), 73 and 78 percent of the participants were born in their place of residence. For women in Punta Gorda and Trujillo this percentage is higher, with 74 percent in Punta Gorda, and 83 percent in Trujillo having been born in their place of residence. In Santa Fe, only 56 percent of the individuals resided where they were born, and only 13 percent of the men that resided in Santa Fe were born there.

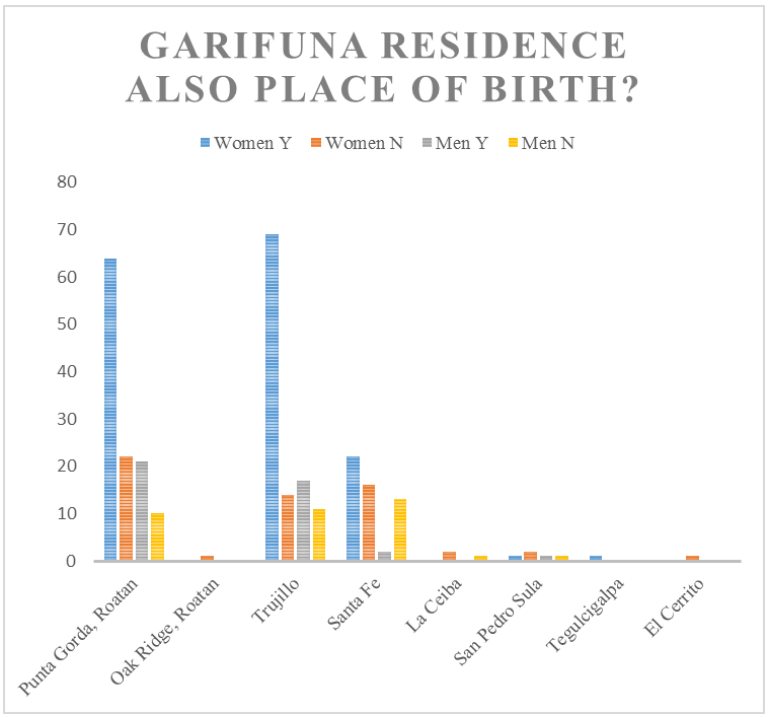

Figure 4.2. Residence as place of birth in male and female Garifuna. Place of residence is along the X axis, and number of individuals is along the Y axis.

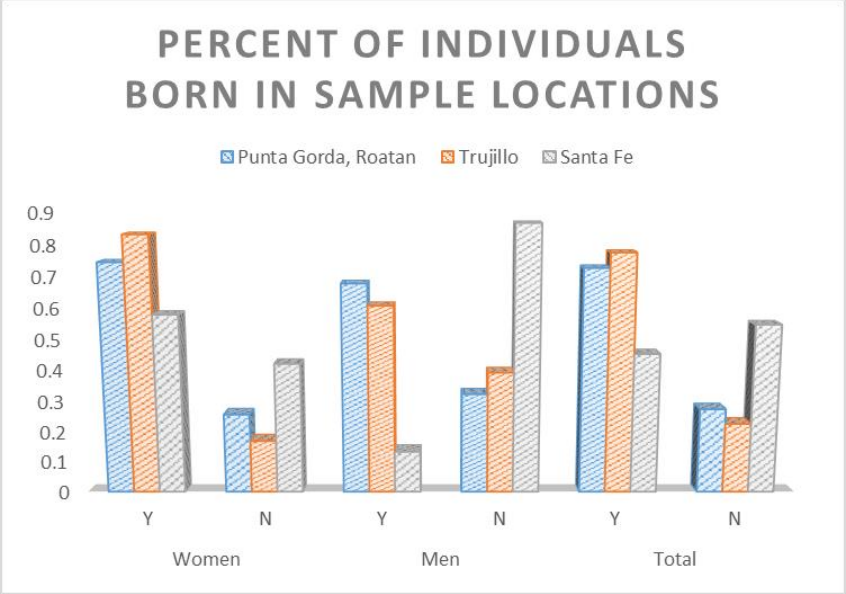

Figure 4.3. Percent of individuals born in Punta Gorda, Trujillo and Santa Fe

MtDNA results

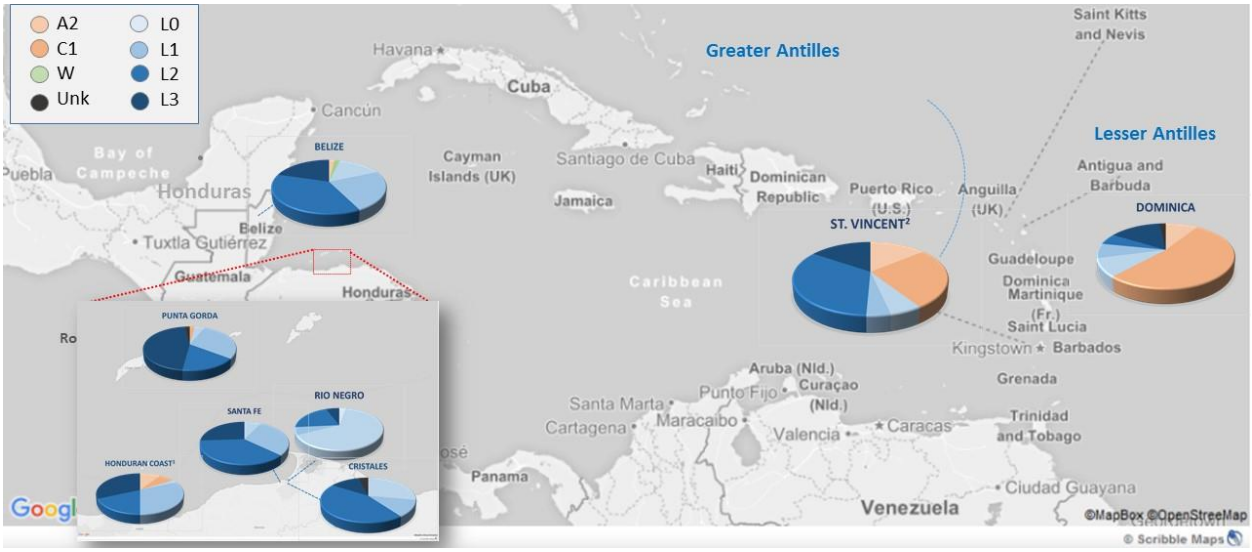

Figure 4.4. MtDNA haplogroups in Garifuna and Kalinago groups of the Caribbean. Native American haplogroups are shown in orange, European haplogroups in green, and African haplogroups in blue. [1]The Honduran Coast sample is from Salas et al. (2005); [2]St. Vincent data from this study combined with St. Vincent data from Benn Torres et al. (2015).

MtDNA haplotypes and haplogroups for the villages of Rio Negro, Cristales, Santa Fe, and Punta Gorda, Roátan, are in Appendix B. Forty-eight mtDNA sequences were characterized from Punta Gorda, which resulted in 31 haplotypes (Appendix B, Table 4.2). Punta Gorda had the most haplogroups represented, including African haplogroups L0, L0a2, L1, L1b, L1b1, L2a, L2a1, L2c, L2c/d, L3, and L3e1. The majority of the African haplotypes belonged to haplogroup L3e1 (44%) (Figure 4.4). One individual from Punta Gorda carried a non-African haplotype belonging to haplogroup A2 (2%). The sample from Rio Negro included 34 individuals with 24 haplotypes. All of the sequences were of an African origin, belonging to haplogroups L0, L0a2, L1b1, L2a1, L2c, L3d and L3e1, with L0a2 the most frequent haplogroup representing 50 percent of the samples. In Barrio Cristales, 25 individuals were characterized with 17 unique haplotypes belonging to African haplogroups L0, L1b1, L2, L2a1, L3d, and L3e1

with most of the lineages belonging to L2a1 (32%) or LO (28%). As with the other coastal villages included in this study, all 27 samples (20 unique haplotypes) in Santa Fe belonged to African lineages. The haplogroup composition included L0, L1, L1b1, L1c1, L2a, L2b, L2c, and L3e1, with the majority of haplotypes belonging to mtDNA haplogroups L2a (30%) and L3e1 (26%).

The additional sequencing of samples from Belize, Dominica and St. Vincent were also completed and haplotypes and haplogroup assignments are included in Appendix B (Table 4.2). On the island of St. Vincent, 30 mtDNA sequences were characterized for HVS-I and HVS-II. Of these, 43 percent of the sequences belonged to Amerind haplogroups A2 (10%) and C1 (33%), and 57 percent represented African haplogroups L1b1, L2a, L2a1, L2b, L2e, L3. The most frequent African haplogroup was L2a1 making up 27 percent of the total sample. From the Kalinago Reserve in Dominica, 53 samples were characterized, with 45 haplotypes. Of these, Amerind haplogroups A2 (10%) C1 (57%) were found in 67 percent of the participants. African haplogroups L1b, L1c1, L2a, L2a1, L2b, L3b, L3b/d, and L3e2 were represented, with the L3e2 making up (12%) of all the sample from Dominica. Fifty-four Garifuna from Belize were also sequenced for HVS-II for inclusion in this study. One individual carried an Amerind haplotype belonging to haplogroup A2 (2%). African lineages found in Belize included L0a2, L1b1, L1c0, L2a, L2a1, L3e1a, L3f1. The highest frequencies of African lineages were found with haplogroups L1b1 (20%), L2a (19%) and L2a1 (19%). There was also a single haplotype that belonged to the Eurasian haplogroup W1g (Figure 4.2; Table 4.3).

Table 4.2. Number of haplotypes assigned to mtDNA haplogroups in Garifuna and Kalinago groups. All Honduran Coast includes Cristales, Rio Negro, Santa Fe and data from Salas et al. (2005).

Haplogroup	Punta Gorda	Cristales	Rio Negro	Santa Fe	Honduran Coast[1]	All Honduran Coast	Belize	St. Vincent	St. Vincent[2]	All St. Vincent	Dominica
A2	1 (2%)				4 (9%)	**5 (4%)**	1 (2%)	3 (10%)	7 (16%)	**10 (14%)**	5 (10%)
C1					3 (7%)	**3 (2%)**		10 (33%)	9 (21%)	**19 (26%)**	29 (57%)
L0	1 (2%)	7 (28%)	5 (15%)	2 (7%)		**14 (11%)**			4 (9%)	**4 (6%)**	
L0a2	1 (2%)		17 (50%)		1 (2%)	**18 (14%)**	8 (15%)				
L1	1 (2%)			1 (4%)		**1 (1%)**			2 (5%)	**2 (3%)**	
L1b	1 (2%)										1 (2%)
L1b1	5 (10%)	3 (12%)	2 (6%)	6 (22%)	12 (27%)	**23 (17%)**	11 (20%)	1 (3%)		**1 (1%)**	
L1c0	7 (15%)						2 (4%)				
L1c1				1 (4%)	2 (5%)	**3 (2%)**					4 (8%)
L2		3 (12%)				**3 (2%)**			12 (28%)	**12 (17%)**	
L2a	1 (2%)			8 (30%)		**8 (6%)**	10 (19%)	4 (13%)		**4 (6%)**	1 (2%)
L2a1	1 (2%)	8 (32%)	2 (6%)	1 (4%)	8 (18%)	**19 (15%)**	10 (19%)	8 (27%)		**8 (11%)**	1 (2%)
L2b								1 (3%)		**1 (1%)**	1 (2%)
L2c	4 (8%)		4 (12%)	1 (4%)		**5 (4%)**					
L2c/d	1 (2%)										
L2c2	1 (2%)		1 (3%)			**1 (1%)**					
L2e								1 (3%)		**1 (1%)**	
L3	1 (2%)								9 (21%)	**9 (13%)**	
L3b								2 (7%)		**2 (3%)**	
L3d		1 (4%)	1 (3%)			**2 (2%)**					1 (2%)
L3b/d											1 (2%)
L3e1	21 (44%)	2 (8%)	2 (6%)	7 (26%)		**11 (8%)**					
L3e1a					3 (7%)	**3 (2%)**	4 (7%)				
L3e2					9 (20%)	**9 (7%)**					6 (12%)
L3f1					2 (5%)	**2 (2%)**	7 (13%)				
W1g							1 (2%)				
Unk	1 (2%)	1 (4%)				**1 (1%)**					1 (2%)
Total hts	**48**	**25**	**34**	**27**	**44**	**130**	**54**	**30**	**43**	**72**	**51**

[1]Salas et al. 2005

[2]Benn-Torres et al. 2015

Summary statistics for all Garifuna and Kalinago communities in this study and in the literature are shown in Table 4.3. The highest gene diversity is found in the 51individuals in Dominica (0.9877), which also has the highest expected diversity based on the expected number of alleles and the number of segregating sites (See Figure 4.5). Dominica is also the only sample that has significant values for Tajima's D (-1.60175, p = 0.025) and Fu's Fs (-21.0609, p = 0.000), indicating the population may be undergoing an expansion. Punta Gorda in Roatan displays the greatest mean number of pairwise differences (16.3307), the greatest diversity of

loci (0.0234), and the highest expected diversity estimated by gene diversity (Figure 4.5). Cristales, on the Honduran coast, displays the lowest level of pairwise differences (11.0567) and the lowest diversity of loci (0.0158). When compared to all other Garifuna and Kalinago groups, the population from the Honduran Coast (Salas A. , et al., 2005), displayed the lowest levels of gene diversity (0.8911), as well as estimates of expected diversity calculated by gene diversity, the number of expected alleles, and diversity by the number of segregating sites (Figure 4.4).

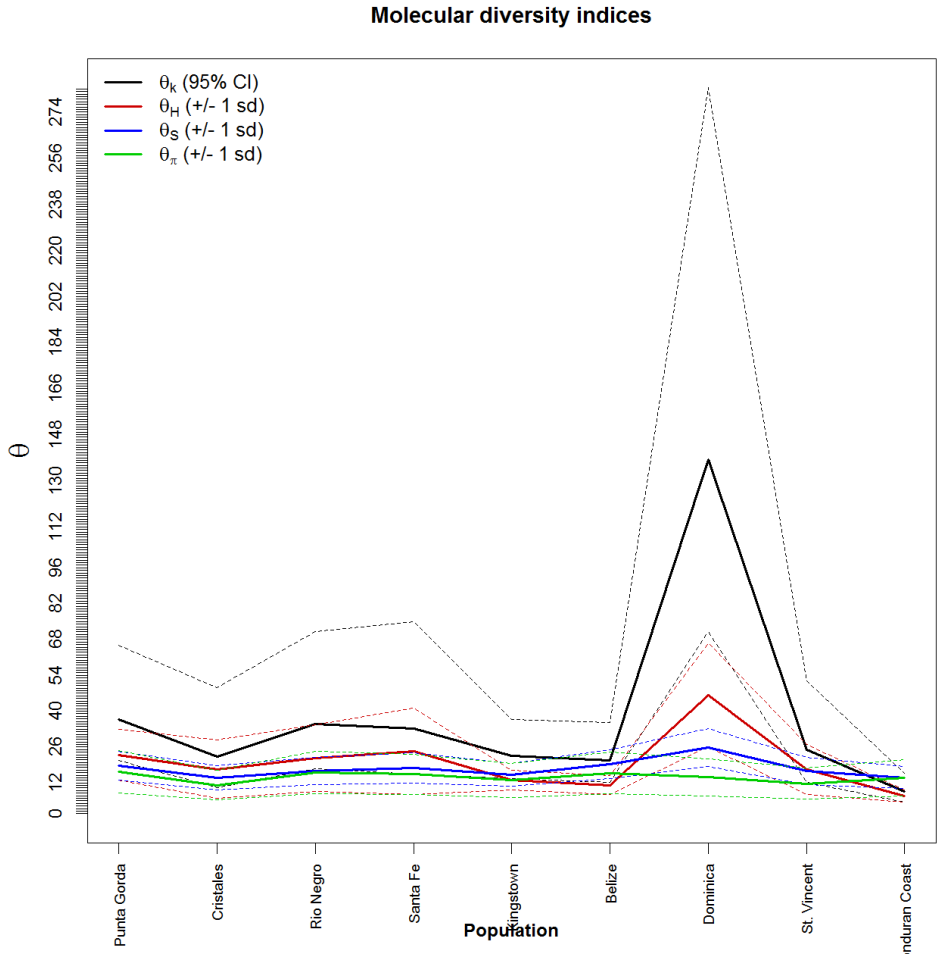

Figure 4.5. Molecular diversity indices for Garifuna and Kalinago communities in the Caribbean and Central America. Note that the expected diversity (θ_π) equals the mean number of pairwise differences (π).

*	Population	n	# ht	H	+/-	π	+/-	π_n	+/-	ϑ_H	S.D. ϑ_H	ϑ_k	95% CI for θ_k	ϑ_S	S.D. ϑ_S	Tajima's D	p	Fu's Fs	p
Garifuna/Black Carib	St. Vincent	30	20	0.9494	0.0255	11.6874	5.4452	0.0167	0.0087	17.1592	9.7682	25.0555	12.3531, 51.9361	16.6597	5.4453	-1.14086	0.1290	-3.0628	0.1590
	Kingstown, St. V	65	31	0.9361	0.0158	12.9659	5.9150	0.0187	0.0094	13.1190	3.7518	22.6105	13.7937, 36.8825	15.1774	4.3053	-0.50927	0.3540	-3.5471	0.1840
	Dominica	53	45	**0.9877**	0.0083	14.2083	6.4714	0.0204	0.0103	78.1568	54.7516	**138.1763**	71.1125, 283.5795	**25.7820**	7.3420	**-1.60175**	0.0250	**-21.0609**	0.0000
	Punta Gorda, Roátan	48	31	0.9610	0.0150	16.3307	7.4043	**0.0234**	0.0118	**22.9386**	9.8480	36.7796	20.8218, 68.8096	18.7023	5.2587	-0.4978	0.3650	-4.8660	0.0800
	Cristales	25	17	0.9500	0.0293	**11.0567**	5.1984	**0.0158**	0.0083	17.3824	11.4955	22.1396	10.2527, 49.1262	14.0362	4.8234	-0.8193	0.2390	-2.3177	0.1690
	Rio Negro	34	24	0.9590	0.0220	**16.1016**	7.3591	0.0231	0.0117	21.7083	12.9487	34.9743	17.6831, 71.1147	16.6308	5.2986	-0.14397	0.5000	-3.3520	0.1260
	Santa Fe	27	20	0.9630	0.0234	15.3390	7.0724	0.0220	0.0113	24.2876	16.8667	33.3118	15.3994, 75.0657	17.9015	5.9561	-0.58229	0.3240	-2.6969	0.1590
	Honduran Coast	44	16	**0.8911**	0.0300	13.9186	6.3667	0.0200	0.0102	**6.9440**	2.3596	**8.5981**	4.5848, 15.7964	**14.0230**	4.3005	-0.04889	0.5380	2.8025	0.8450
	Belize	54	27	0.9266	0.0212	15.9147	7.2093	0.0228	0.0115	11.1717	3.8026	20.8256	12.1890, 35.1471	19.3113	5.5691	-0.06234	0.2950	-1.2587	0.3720

Diversity measures on HVS-I sequences (nps 16024-16400) and HVS-II sequences (nps 80-400). The number of samples (n), the number of unique haplotypes (#hts), Nei's gene diversity (H), mean number of pairwise differences (π), average diversity of loci (π_n), expected diversity estimated by gene diversity (θ_H), expected diversity estimated using expected number of alleles (θ_k), expected diversity estimated using segregated sites (θ_S), Tajima's , and Fu's Fs. Highest values are shown in red, lowest values in blue. Significant Tajima's D and Fu's Fs values shown in red and bold.

Table 4.3. Summary statistics for Garifuna and Kalinago populations in the Caribbean.

Mismatch distributions were computed for all Garifuna and Kalinago communities (Figure 4.6) and for all of the Honduran coastal communities combined (Figure 4.7). The mismatch distribution of all communities found on the Honduran Coast appear unimodal ($r = 0.050$, $p = 0.18$), with some evidence of demographic expansion. The Kalinago of Dominica display a unimodal distribution, with a small raggedness index ($r = 0.0025$, $p = 1.00$), suggestive of a demographic expansion, as supported by Tajima's D and Fu's FS values. The Honduran Coast ($r = 0.0367$, $p = 0.00$), Belize ($r = 0.0218$, $p = 0.00$), and Cristales ($r = 0.0371$, $p = 0.07$) populations exhibit multimodal distributions with high raggedness values and small p values, indicating populations that have not undergone recent expansion events. The other populations fall somewhere in between, with raggedness indices between 0.010 – 0.017, and p values between 0.10 and 0.53 (Figure 4.6). In addition, a Mantel test was performed to test the relationship of mtDNA distances in Garifuna groups versus the geographic distance between groups. MtDNA distances displayed a correlation with geographic distances ($r=0.4629$, $p=0.0129$).

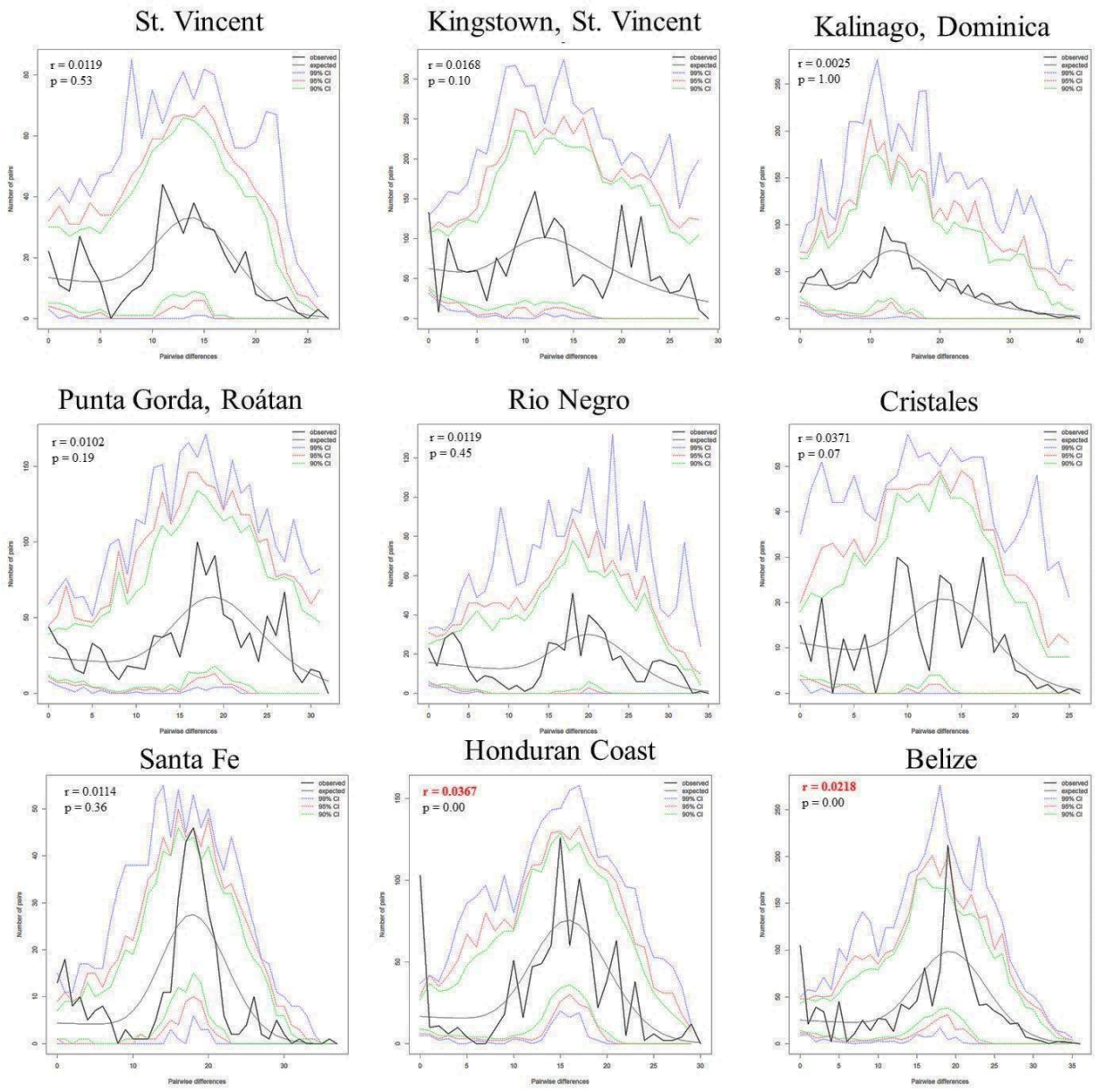

Figure 4.6. MtDNA mismatch distributions for HVS-I and II sequences in Garifuna and Kalinago locations, including Kingstown St. Vincent (Benn Torres, et al., 2015) and the Honduran Coast (Salas A. , et al., 2005). Thick black line represents observed mismatches, thin black line represents expected, blue dashed line represents a 99% confidence interval, red dashed line represents a 95% confidence interval, and a green dashed line represents a 90% confidence interval.

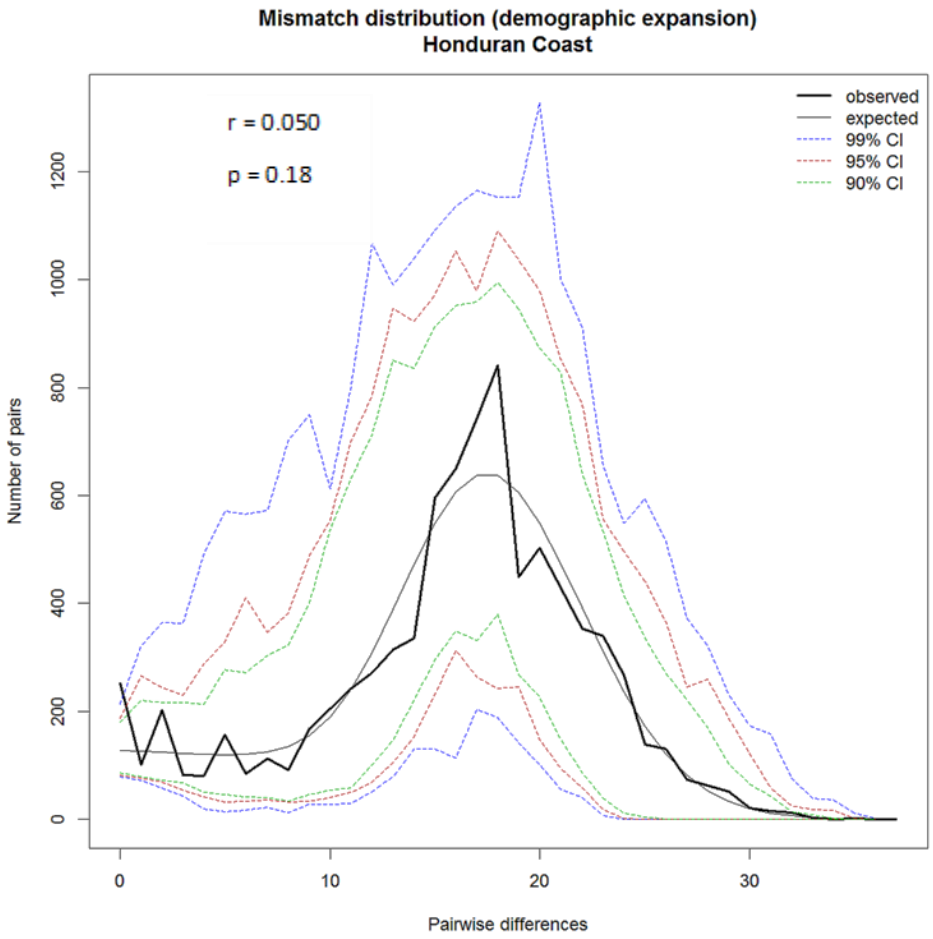

Figure 4.7. Mismatch distribution for the Honduran Coast, including the communities of Cristales, Rio Negro and Santa Fe.

Intrapopulation measures between the Carib and Garifuna groups are shown in Figure 4.9. Nei's net number of nucleotide differences were smallest between the communities of Santa Fe, just west of the Honduran city of Trujillo, and the population from the Honduran Coast (sampled by Salas et al., 2005), and Santa Fe compared to Punta Gorda, on Roátan. The highest net number of nucleotide differences were seen between Rio Negro, in Trujillo, and St. Vincent in the Lesser Antilles, between and Rio Negro and Dominica, also in the Lesser Antilles. The average number of pairwise differences between populations was lowest between St. Vincent

and Cristales, and the highest were found in comparison with Rio Negro, which showed a high average number of pairwise differences between Dominica and Punta Gorda. The comparison of Dominica and Punta Gorda and between Santa Fe and Rio Negro also showed a high number of average pairwise difference. The MDS plot based on Tamura and Nei's genetic distances between populations show a separation of the Lesser Antilles populations. Most of the coastal communities form a cluster together towards the center of the plot. Rio Negro, with nearly 50 percent of its lineages belonging to haplogroup L0a2, is pulled to farthest right corner of the plot, away from all other villages (Figure 4.8)

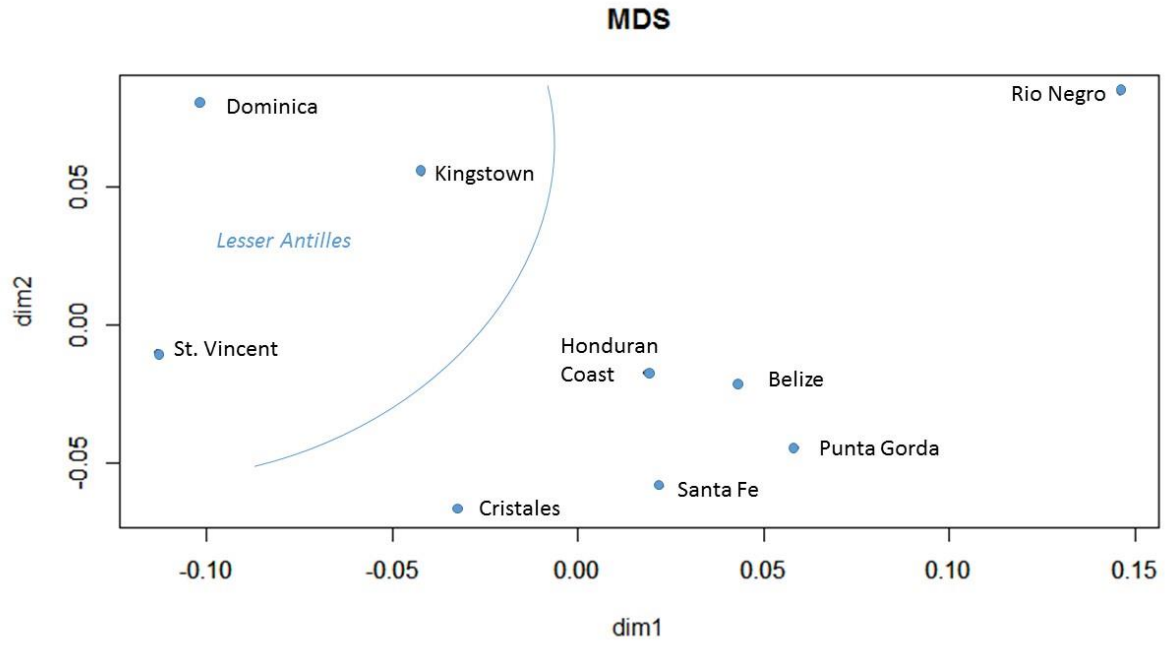

Figure 4.6. Multidimensional scaling plot of Tamura and Nei's distances of mtDNA sequences in 9 Garifuna and Kalinago Villages.

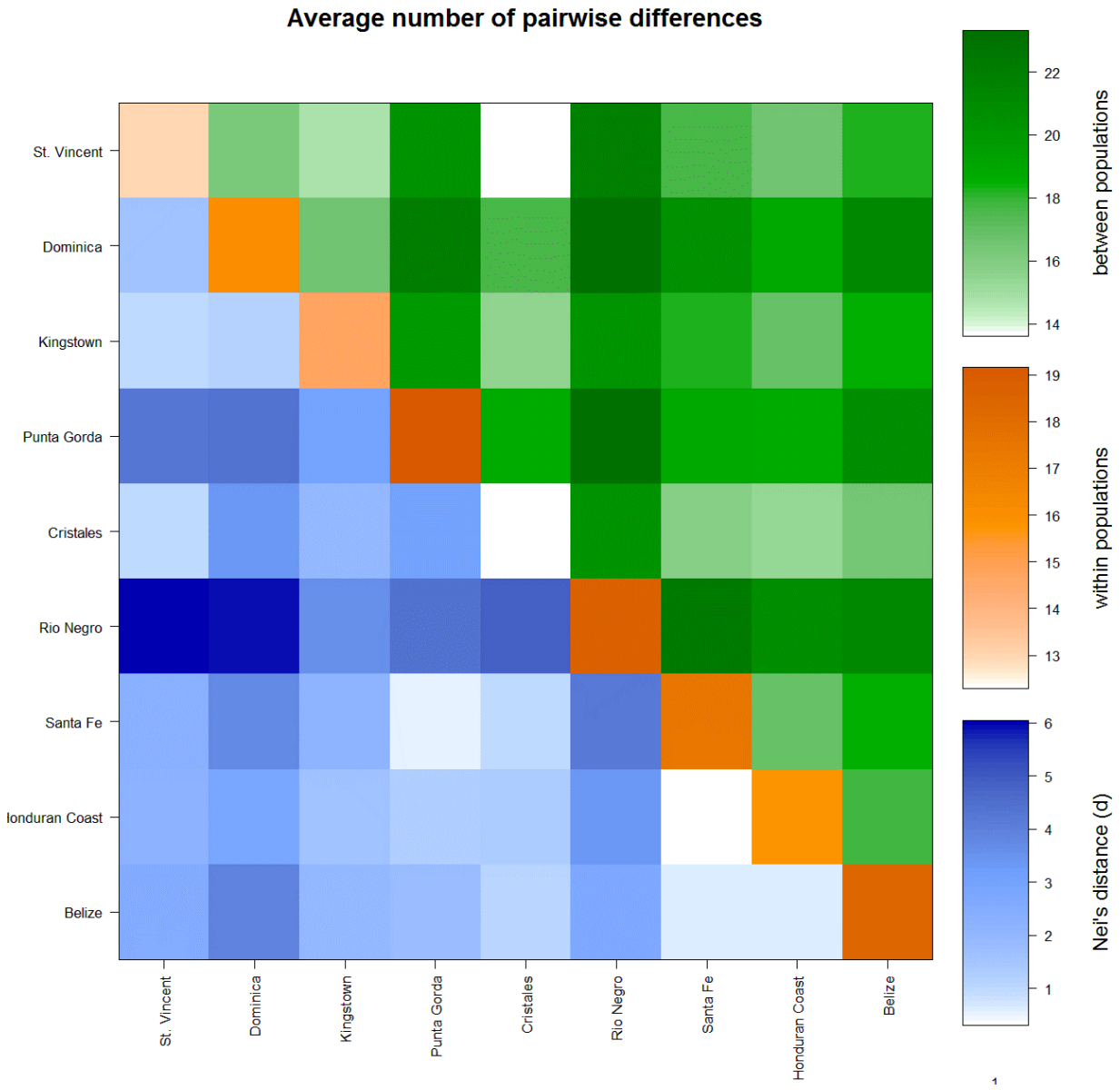

Figure 4.7. Heat map of the average number of pairwise differences within populations (orange), between populations (green), and net number of nucleotide differences between populations (blue), using mtDNA HVS-I and II sequences from 9 Garifuna and Black Kalinago locations.

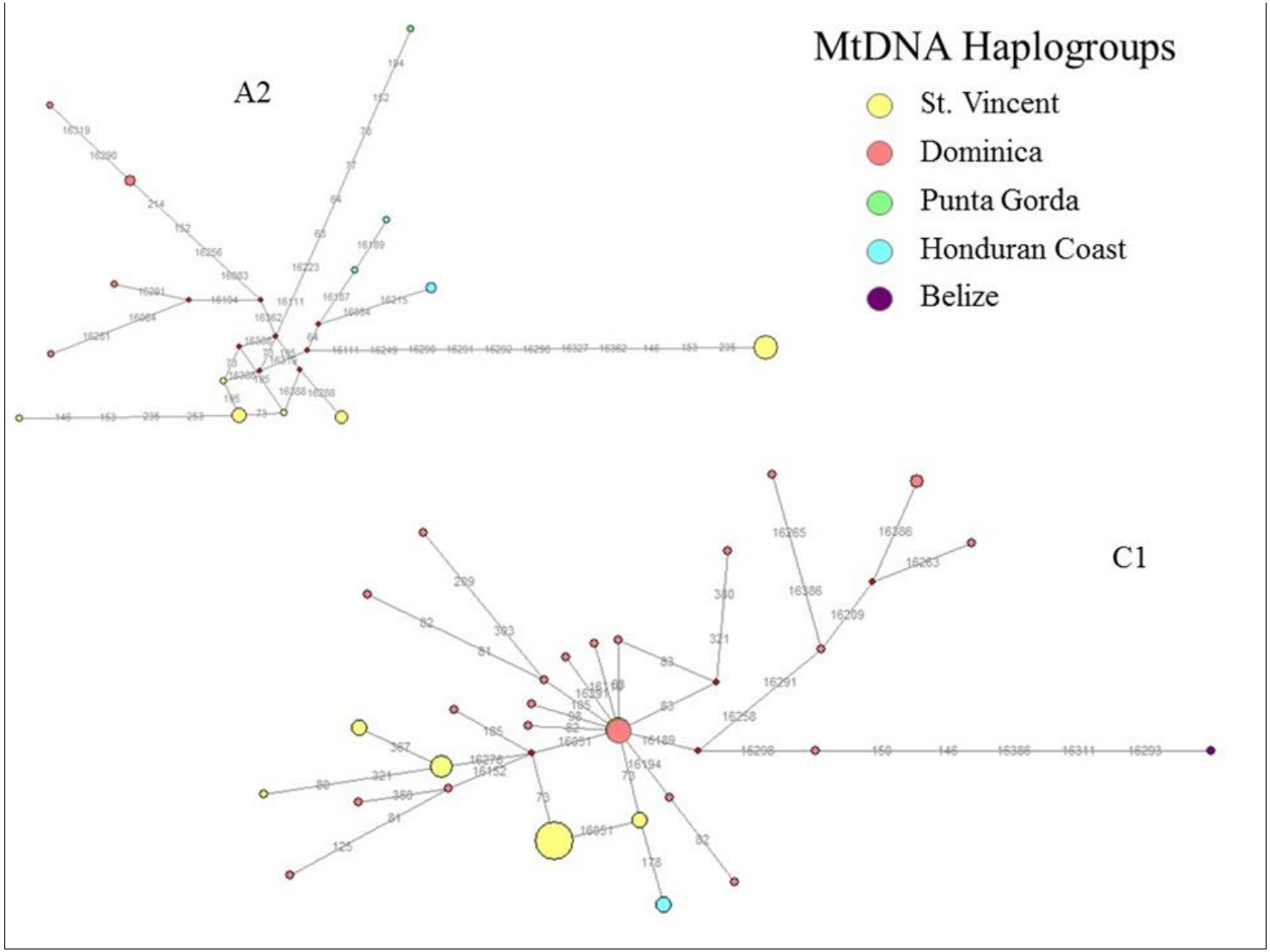

Figure4.8 Networks of haplogroups A2 and C1 in Garifuna, including St. Vincent samples from Benn Torres (2015), and Kalinago communities from Dominica.

A Network of native mtDNA haplogroups A2 and C1 are shown in Figure 4.10. Of the few Native American haplotypes found on the Honduran Coast and Punta Gorda, none were shared with the Lesser Antilles. However, the three C1 haplotypes found on the Honduran Coast were closely related to haplotypes on St. Vincent, with only a single mutation away from the nearest haplotypes in the network. The C1 haplotype in Belize, was different from all haplotypes in the network, with the nearest haplotype from Dominica 5 steps away. The four A2 haplotypes found in Punta Gorda and the Honduran Coast were also distinct from the haplotypes found in St. Vincent and Dominica, with the three haplotypes on the Honduran Coast related by a common node that was 1 or 2 mutational steps away; the haplotype found in Punta Gorda was distinct from the other haplotypes, and the nearest relation in the network was 11 mutations away.

MtDNA networks were also constructed for the 4 African macrohaplogroups L0, L1, L2, and L3 (Figure 4.11 and 4.12). Most haplogroups (L0, L1, L3) display networks with St. Vincent and Dominica haplotypes forming separate, distant branches from the haplotypes found in the coastal communities. St. Vincent haplotypes (including haplotypes from Benn-Torres et al. (2015) belonging to haplogroup L0 formed a separate branch from the other L0 haplotypes found in Garifuna on the Honduran coast and Punta Gorda (Figure 4.11). No L0 haplotypes were shared between groups, however many related L0a2 haplotypes are a single mutation away from a L0a2 haplotype in Punta Gorda. This cluster also included two nodes of haplotypes from Belize. The haplotypes from Cristales were distinct from the other L0 haplotypes. Haplotypes that belonged to haplogroup L1 also displayed distinct branches of haplotypes found in St. Vincent and Dominica. Several nodes were shared between the coastal communities and Punta Gorda including a node of L1c1 haplotypes found in Punta Gorda and Cristales. Other L1

haplotypes found in Punta Gorda were also found in Santa Fe, Cristales, and Rio Negro. The L3 network shows distinct branches of St. Vincent and Dominica L3 haplotypes, with a two related haplotypes from Rio Negro and the Honduran coast 2 steps away (Figure 4.12). There is one L3e1 node that is shared by Punta Gorda with the communities of Santa Fe and the Honduran coast. Two other nodes, one shared by Punta Gorda and Rio Negro, and another by Cristales and Rio Negro, are also found in the network. A few nodes from Belize share similarities with haplotypes from the Honduran coast, and are 2 steps away from them.

MtDNA Haplogroup L2 was the only haplogroup that displayed nodes shared by St. Vincent and Garifuna villages on the coast (Figure 4.12). While several branches of L2 haplotypes in Figure 4.11 were offshoots of St. Vincent and Dominica haplotypes, this L2 network also shows cluster of related L2a1 haplotypes that are shared or closely related to St. Vincent haplotypes. This includes a large node of a haplotype that is shared by St. Vincent, Rio Negro, Cristales, Santa Fe, Belize, and the Honduran Coast (Salas A. , et al., 2005). A separate node shows a shared haplotype between St. Vincent and Punta Gorda. Several haplotypes found in Belize were only 1 or two steps away from those found in Honduras. And, another L2a node, a single step away from a haplotype found on St. Vincent, is shared by Punta Gorda, Cristales, Santa Fe, the Honduran Coast, and Belize.

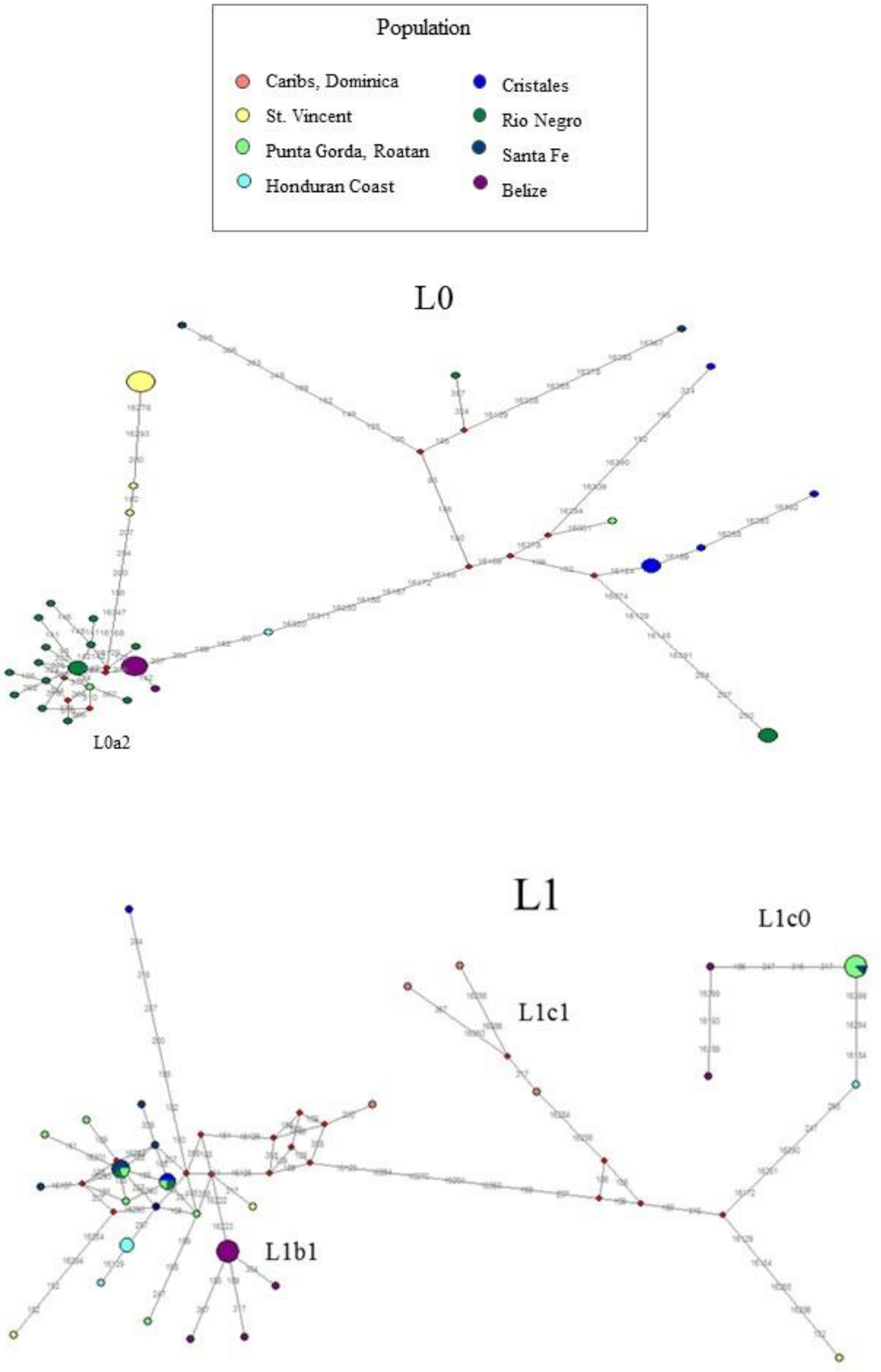

Figure 4.9. Networks of Garifuna and Kalinago haplotypes belonging to haplogroups L0 and L1.

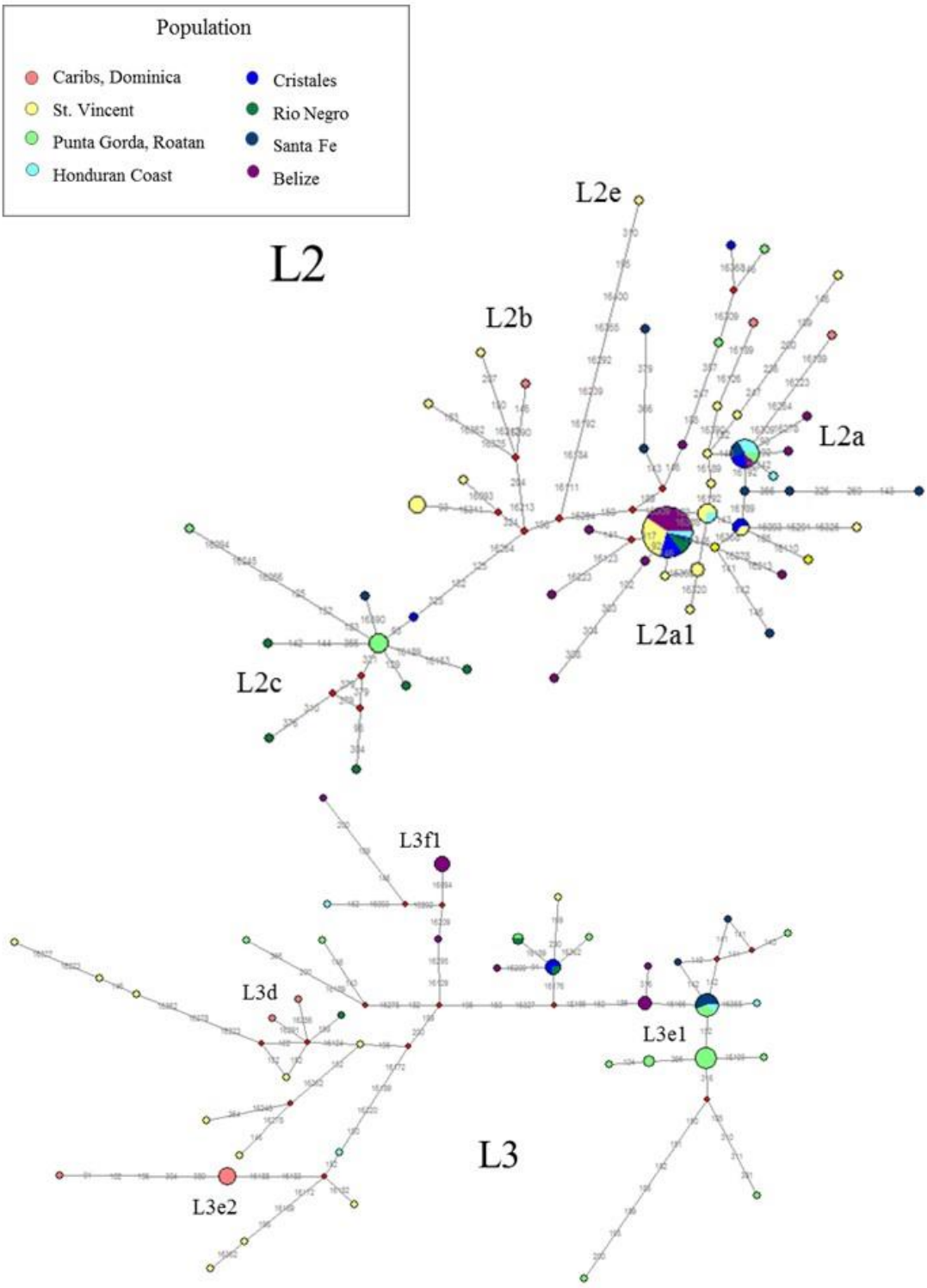

Figure 4.10. Network of Garifuna and Kalinago haplotypes belonging to haplogroups L2 and L3.

Table 4.4. AMOVA of Garifuna and Kalinago communities grouped by geography: Lesser Antilles (St. Vincent and Dominica), Punta Gorda, the Honduran Coast (including Rio Negro, Cristales, and Santa Fe), and Belize.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation
Among Groups	3	267.744	0.42554 Va	4.47
Among pops. w/in groups	5	214.276	.91132 Vb	9.57
Within populations	371	3038.517	8.19007 Vc	85.97
Total	379	3520.537	9.5694	

*Red indicates $p \leq 0.000$ +/-0.000

An AMOVA analysis based on Geography was performed to examine the population structure of communities in the Lesser Antilles, Punta Gorda, the Honduran Coast, and in Belize (Table 4.4). Most of the variation, 85.97 percent, was found within the communities examined. The variation between communities within groups explained 9.57 percent of the variation, and the other 4.47 percent of the variation could be explained by the variation between the geographic groupings of the communities.

Summary statistics for all populations included in this study are shown in Table 4.5. All of the Garifuna communities displayed a gene diversity that was lower than most of the African groups, excluding the small sample from the Bight of Biafra, as well as admixed populations in Central and South America. The mean number of pairwise differences and the average diversity of loci in Garifuna and Kalinago groups were higher than that seen in most other populations except for those found in West Central Africa. The expected diversity measures of Garifuna groups were intermediate between those found in Africa and Central/South America. The Cariban Speakers of Panama displayed the lowest level of diversity in all measures computed.

The highest diversity measures were found in West Central Africa and the Choco sample, an admixed population of largely African ancestry found in Columbia. Expected levels of diversity in all populations are plotted in Figure 4.10.

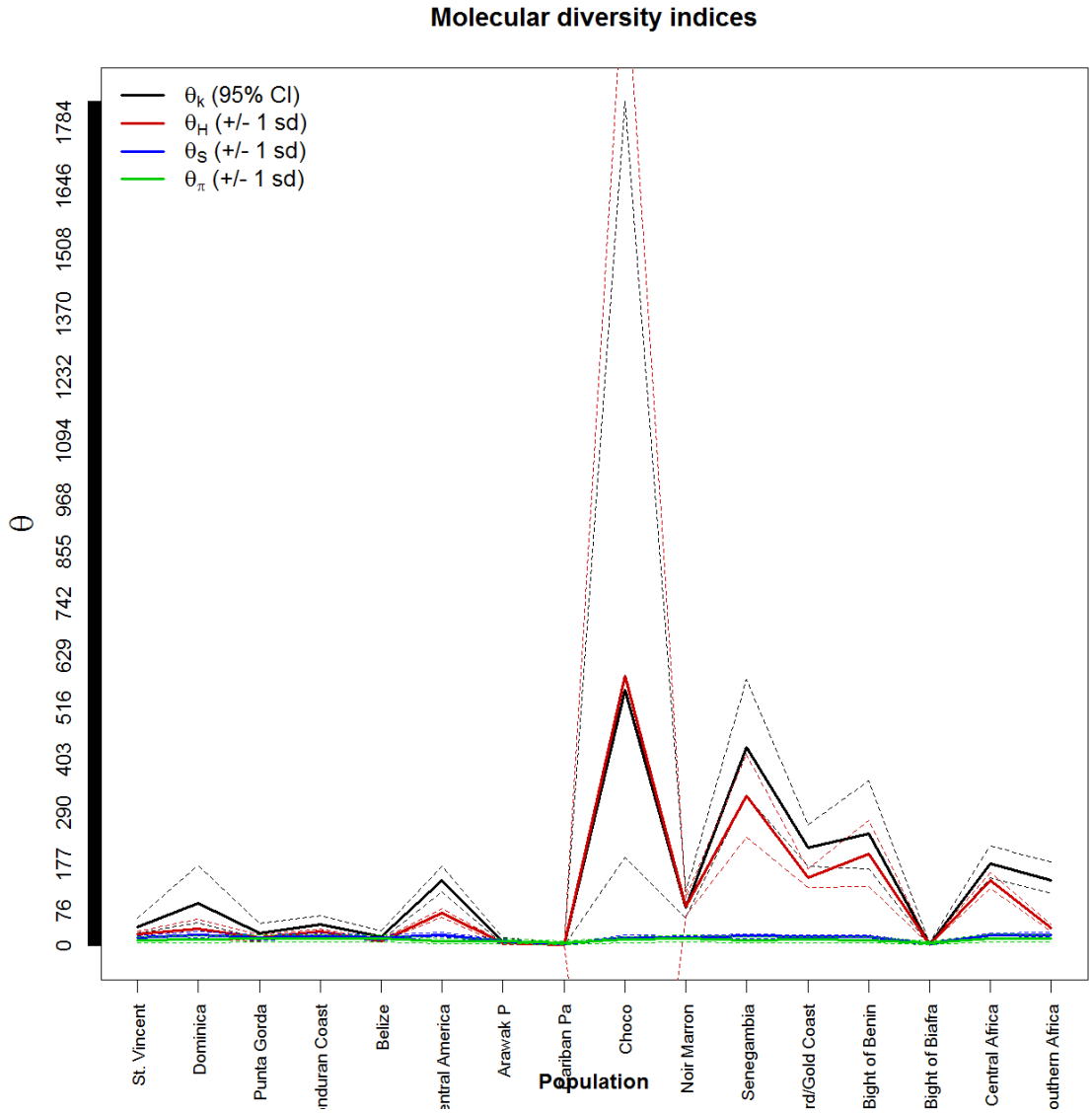

Figure 4.11. Expected diversity measures using mtDNA HVS-I and II sequence in Garifuna, Kalinago, Central and South American, and African populations.

*	Population	n	# ht	H	+/-	π	+/-	π_n	+/-	θ_H	S.D. θ_H	θ_k	95% CI for θ_k	θ_S	S.D. θ_S	Tajima's D	p	Fu's Fs	p
Garifuna/Black Carib	St. Vincent	95	49	0.9639	0.0083	12.6670	5.7621	0.0193	0.0097	25.0132	6.2990	39.9813	26.5382, 60.1656	17.1680	4.5181	-0.8711	0.1900	**-14.9061**	0.0100
	Dominica	53	42	0.9746	0.0141	13.6909	6.2470	0.0207	0.0105	36.5710	21.7155	91.5676	49.9436, 174.2215	24.0192	6.8644	**-1.5214**	0.0410	**-19.9119**	0.0000
	Punta Gorda, Roátan	48	28	0.9495	0.0171	16.1241	7.3145	0.0244	0.0123	17.1757	6.5689	27.2470	15.5322, 48.0463	18.0263	8.1187	-0.4153	0.3900	-2.6940	0.2070
	Honduran Coast	130	62	0.9699	0.0054	15.8248	7.1053	0.0239	0.0119	30.5089	5.9398	45.8409	32.1132, 65.26618	22.0552	5.4160	-0.9530	0.1680	**-16.8592**	0.0050
	Belize	54	26	0.9245	0.0210	15.5507	7.0515	0.0235	0.0118	10.8068	3.5494	19.0861	11.1428, 35.5194	18.2141	5.2727	-0.5187	0.3620	-0.8886	0.4290
Central/ South America	Central America	475	209	0.9865	0.0016	10.0573	4.6051	0.0153	0.0077	71.1696	9.0194	142.0151	117.1609, 171.9183	23.7407	4.8035	**-1.7559**	0.0050	**-23.8541**	0.0090
	Arawak Speakers (Peru)	29	13	0.8719	0.0429	10.1823	4.7884	0.0155	0.0081	5.6702	2.3945	8.4824	4.1095, 17.2611	9.9308	3.4075	0.0937	0.6100	1.0488	0.6960
	Cariban speakers (Panama)	46	9	**0.7729**	0.0416	**6.1169**	2.9638	**0.0094**	0.0050	**2.6651**	0.6778	**3.0677**	1.4321, 6.2442	**3.8681**	1.4041	1.8405	0.9740	3.5338	0.8750
	Choco (Columbia)	49	47	**0.9983**	0.0046	13.1803	6.0334	0.0199	0.0101	**585.0136**	1578.7676	**555.8912**	192.5891, 1832.1211	18.3906	5.4184	-1.0109	0.1540	**-24.3772**	0.0000
	Noir Marron (French Guiana)	142	83	0.9886	0.0025	15.2227	6.8429	0.0203	0.0115	84.9063	19.5326	82.7564	58.9928, 116.3543	17.7231	4.3604	-0.4492	0.3740	**-23.9701**	0.0000
Africa	Senegambia	267	208	0.9970	0.0008	12.6045	5.7029	0.0191	0.0095	325.8298	89.3363	431.1891	324.7409, 577.5707	21.0950	4.6600	-1.2370	0.0770	**-23.8666**	0.0040
	Windward/Gold Coast	382	219	0.9938	0.0009	13.0475	5.8872	0.0198	0.0099	15.3383	23.2468	212.6632	172.3744, 262.5567	19.7813	4.1797	-1.0161	0.1390	**-23.7137**	0.0050
	Bight of Benin	150	117	0.9951	0.0017	12.6592	5.7402	0.0192	0.0096	200.2211	71.4261	242.8696	167.4106, 357.5664	19.3392	4.6857	-1.0986	0.1040	**-24.0808**	0.0000
	Bight of Biafra	30	8	0.8000	0.0478	6.6207	3.2157	0.0100	0.0054	3.1710	1.0254	3.2259	1.4094, 7.0407	4.5436	1.7210	1.5746	0.9650	3.3250	0.9200
	West Central Africa	468	230	0.9931	0.0008	**16.4912**	7.3576	**0.0249**	0.0123	142.1784	17.0643	178.3416	147.3476, 215.7288	22.7522	4.6273	-0.8186	0.2180	**-23.5025**	0.0110
	Southern Africa	294	160	0.9756	0.0048	15.0730	6.7582	0.0228	0.0113	38.2117	7.9896	142.8185	112.5612, 181.2541	**24.1249**	5.2063	-1.1520	0.1000	**-23.7016**	0.0050

Diversity measures on HVS-I sequences (nps 16050-16400) and HVS-II sequences (nps 90-400). The number of samples (n), the number of unique haplotypes (#hts), Nei's gene diversity (H), mean number of pairwise differences (π), average diversity of loci (π_n), expected diversity estimated by gene diversity (θ_H), expected diversity estimated using expected number of alleles (θ_k), expected diversity estimated using segregated sites (θS), Tajima's , and Fu's Fs. Highest highlighted in red, lowest values in blue. Significant Tajima's D and Fu's Fs values shown in red and bold. Honduran Coast includes: Rio Negro, Cristales, Santa Fe; Central America

Table 4.5. Diversity measures and tests of neutrality in Garifuna, Carib and comparative populations in Central and South America and Africa.

Intrapopulation measures were computed between Garifuna, Carib and other comparative populations (Figure 4.14 and 4.15). The largest differences by net nucleotide differences and average number of pairwise differences from the Garifuna and Caribs from Dominica are in their comparison to the Bight of Biafra. The least net nucleotide and average number of pairwise differences are seen between the Garifuna and African populations from Senegambia, the Windward/Gold Coast, and the Bight of Benin, as well as the Choco from Columbia. African admixed groups from South America were also most similar to African groups besides those from the Bight of Biafra. Arawak and Cariban speaking groups from Central and South America showed little differences between each other. A MDS plot was constructed of Tamura and Nei's genetic distances between populations (Figure 4.15). The plot shows that the Garifuna are most closely related to one another, to African populations, Dominica, and to the Choco in Columbia. The farther left on the plot, the more Native American haplogroups are found within the population. The Kalinago and the Garifuna from Kingstown, St. Vincent are more closely related to one another than to any other group, and they and the St. Vincent sample from the northern villages plot nearest to the groups found in Central America with more Native American haplotypes. Cristales, Rio Negro, and Santa Fe form a cluster in the lower center portion of the plot. The Honduran Coast sample by Salas et al., (2005) appears most closely related to the Bight of Benin and to the Choco of Columbia, while Punta Gorda and Belize appear closest to populations from West Central Africa.

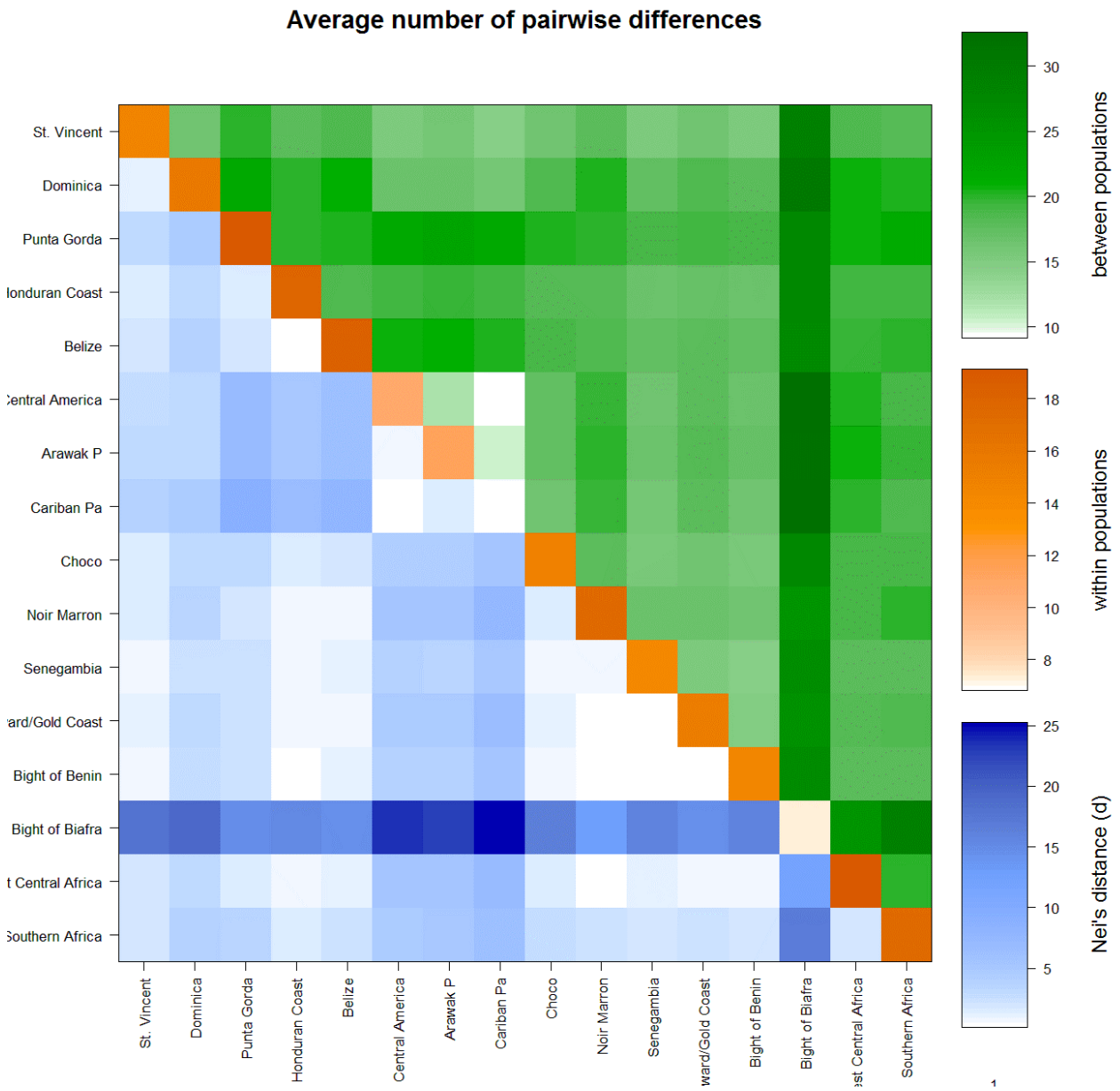

Figure 4.12. Heat map of the average number of pairwise differences. Within populations (orange), between populations (green), and net number of nucleotide differences between populations (blue), using mtDNA HVS-I and II sequences from all populations included in study.

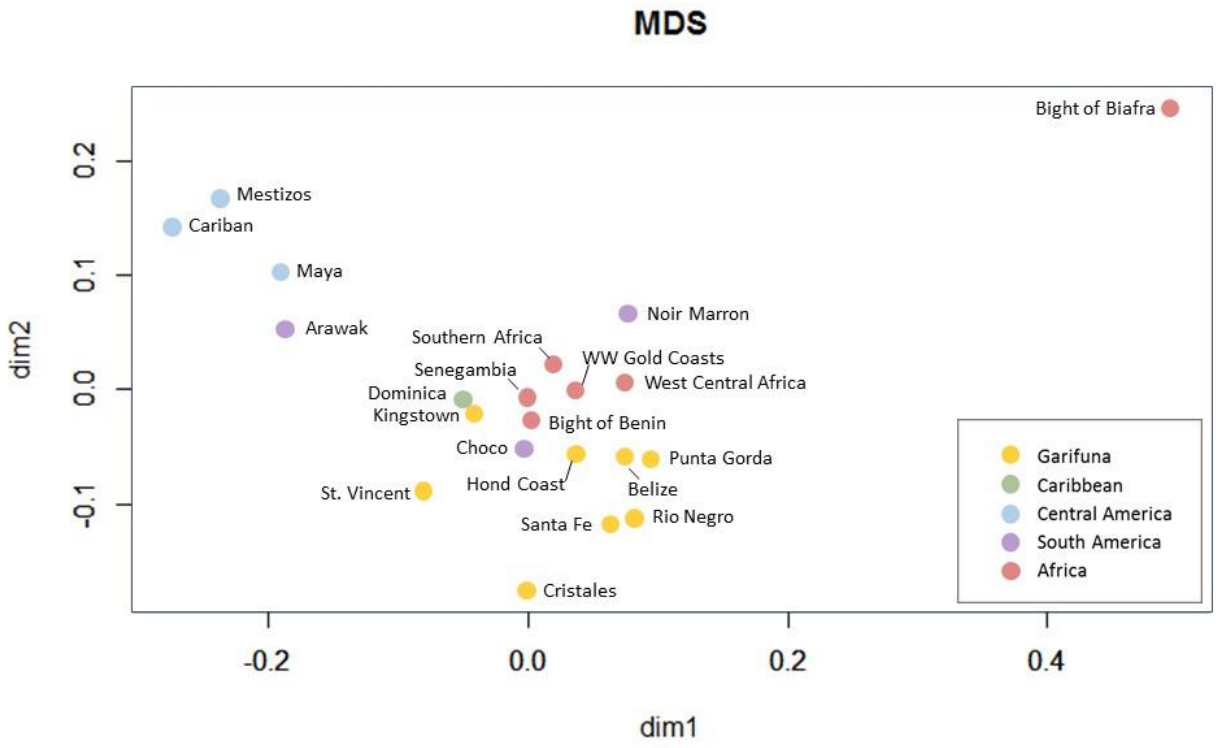

Figure 4.13. MDS plot of Tamura and Nei's genetic distances between Garifuna villages/locations and comparative populations.

Table 4.6. Number of African L2, L3 and L1 haplotypes shared by comparative populations with the Garifuna. Includes St. Vincent data from Benn-Torres et al. (2015) and Salas et al. (2005).

Number of L2 haplotypes shared with Garifuna and Caribs in Central America and the Caribbean

Population	St. Vincent	Punta Gorda	Cristales	Rio Negro	Santa Fe	Honduran Coast	Belize	Central America	Noir Marron	Senegambia	Windward and Gold Coast	Bight of Benin	West Central Africa
St. Vincent*	-		5	2	1	2	11	5	3	4	9	3	2
Punta Gorda		-	1										
Cristales	6	4	-	2	1	1	11		1	1	10	4	1
Rio Negro	6			-	1	1	11		1	1	3	2	1
Santa Fe	6	4			-	3	11		1	3	6	2	1
Honduran Coast	6	1				-	11		1	13	19	7	4
Belize	6		5	2	1	2	-		1	1	3	2	1

Number of L3 haplotypes shared with Garifuna and Caribs in Central America and the Caribbean

Population	St. Vincent	Punta Gorda	Cristales	Rio Negro	Santa Fe	Honduran Coast	Belize	Central America	Noir Marron	Senegambia	Windward and Gold Coast	Bight of Benin	West Central Africa
Dominica											2		
St. Vincent*												3	
Punta Gorda					5	2							
Cristales	6			1									
Rio Negro													
Santa Fe		3				1							
Honduran Coast		3											2
Belize													

Number of L1 haplotypes shared with Garifuna and Caribs in Central America and the Caribbean

Population	St. Vincent	Punta Gorda	Cristales	Rio Negro	Santa Fe	Honduran Coast	Belize	Central America	Noir Marron	Senegambia	Windward and Gold Coast	Bight of Benin	West Central Africa
St. Vincent*													
Punta Gorda			1	2	4					1			2
Cristales		4	-	2	4					1			2
Rio Negro	4				4					1			2
Santa Fe		4								1	2		2
Honduran Coast													
Belize													

Table 4.6 shows the number of haplotypes that were shared with Garifuna by populations in the literature. The Kalinago of Dominica did not share haplotypes with Garifuna from the Lesser Antilles or the Central American Coast. St. Vincent haplotypes belonging to haplogroup L2 were the most commonly shared haplotypes between St. Vincent and Garifuna on the Honduran Coast. Garifuna haplotypes belonging to African macrohaplogroup L2 were also most commonly reported in populations from the Windward and Gold Coasts and Senegambia. L3

haplotypes were only reported in the Windward and Gold Coasts, the Bight of Benin, and West Central Africa. L1 haplotypes were most commonly found in Senegambia and West Central Africa. L0 haplotypes were only found in Rio Negro, and were shared with populations in West Central and Southern Africa.

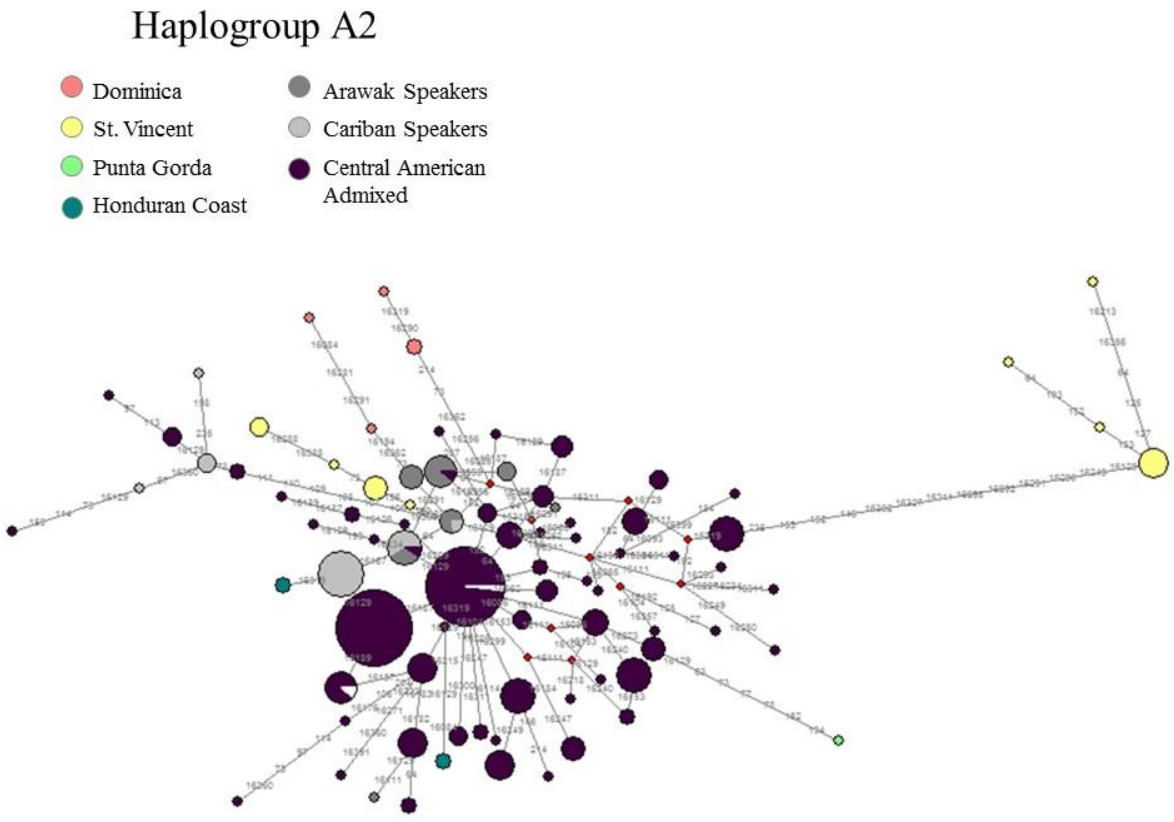

Figure 4.14. Networks of Native American haplogroup A2 including Garifuna, Kalinago, Cariban and Arawak speakers, and Central American haplotypes.

The relationship of Native haplotypes A2 and C1 are visualized in the networks in Figures 4.16 and 4.17. Haplotypes of A2 found in the Garifuna and Caribs form their own branches, with one branch of St. Vincent 7 haplotypes grouped away from other A2 haplotypes (Figure 4.16). The other branches of St. Vincent and Dominica haplotypes are offshoots of Arawak and Cariban speakers' haplotypes. Two nodes, each with 2 haplotypes, represent individuals from the Honduran coast. One A2 haplotype found on the Honduran Coast is shared within a large node of Central American haplotypes found in Maya and Mestizo groups. One node is a single mutation from a large node of Cariban speaking haplotypes. The other node is 3 steps from haplotypes found in neighboring Central American groups. The A2 haplotype from Punta Gorda is distinct from the other haplotypes in the network, but is closest to haplotypes found in Central America. Haplogroup C1 haplotypes from St. Vincent and Dominica form a separate, star-like branch of the network, indicating related haplotypes in an expanding native Caribbean population (Figure 4.17). The two haplotypes that were found on the Honduran Coast form a distant node that is fewer mutations away from St. Vincent haplotypes than any other in the network. However, only four haplotypes belonging to Arawak and Cariban speakers belonged to haplogroup C1, so a relationship between South American haplotypes and the Garifuna is hard to determine from the networks.

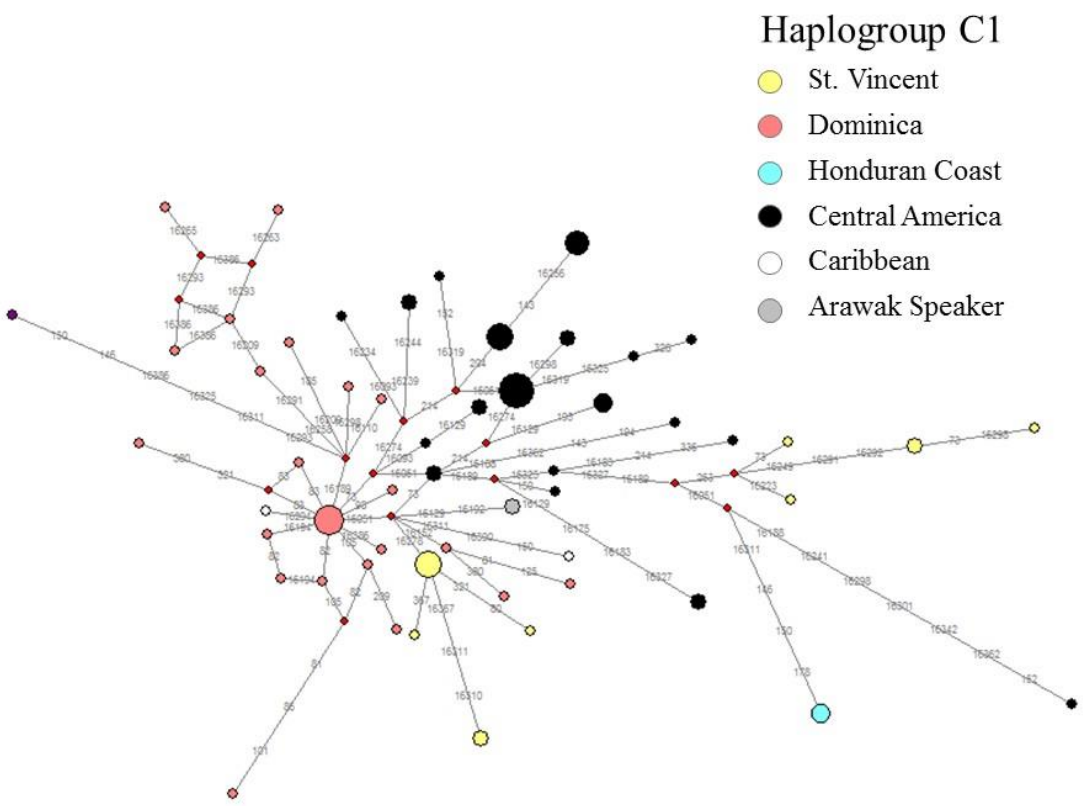

Figure 4.15. Network of haplogroup C1 with Garifuna, Kalinago, and other populations from Central and South America and the Caribbean.

An analysis of molecular variance was computed with groupings based on ancestry, and included Garifuna and Caribs from the Lesser Antilles, Native Caribbean populations, European admixed Central Americans, native groups from Central and South America, African admixed groups from South America, and African populations (Table 4.7). Most of the diversity, 56 percent, could be explained by variation within populations. Thirty-seven percent of the variation could be explained by the variation among groups. Only six percent of the variation could be explained by the variation among populations within groups, indicating that groups of similar admixture were more like one another than groups that may be close geographically.

Table 4.7. AMOVA of Garifuna and Black Caribs from the Lesser Antilles, Punta Gorda, the Honduran Coast, Native Caribbean groups, European admixed Central Americans, Native Central and South Americans, African admixed groups in South America, and Africa.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation
Among Groups	8	8178.578	4.9352	37.43
Among pops. w/in groups	18	1570.285	0.7675	6.39
Within populations	2708	18266.216	6.74528	56.18
Total				

*Red indicates p ≤ 0.000 +/-0.000

An MDS plot was constructed to further examine the relationship of these groups using Tamura and Nei's genetic distances (Figure 4.18). Groups with more Native American lineages group on the right side of the plot. The left side of the plot is skewed by the Bight of Biafra, a small sample that represents a pygmy population. The plot showed a close relationship with the Honduran Coastal populations and the Windward and Gold Coasts, and a further relationship with Senegambia and the Bight of Benin, as well as the Choco of Columbia. St. Vincent and Dominica were again the least distant from one another, but were closest to the African groups from Senegambia and the Bight of Benin. Belize and Punta Gorda appear most closely related to one another, and are found in the lower corner of the plot.

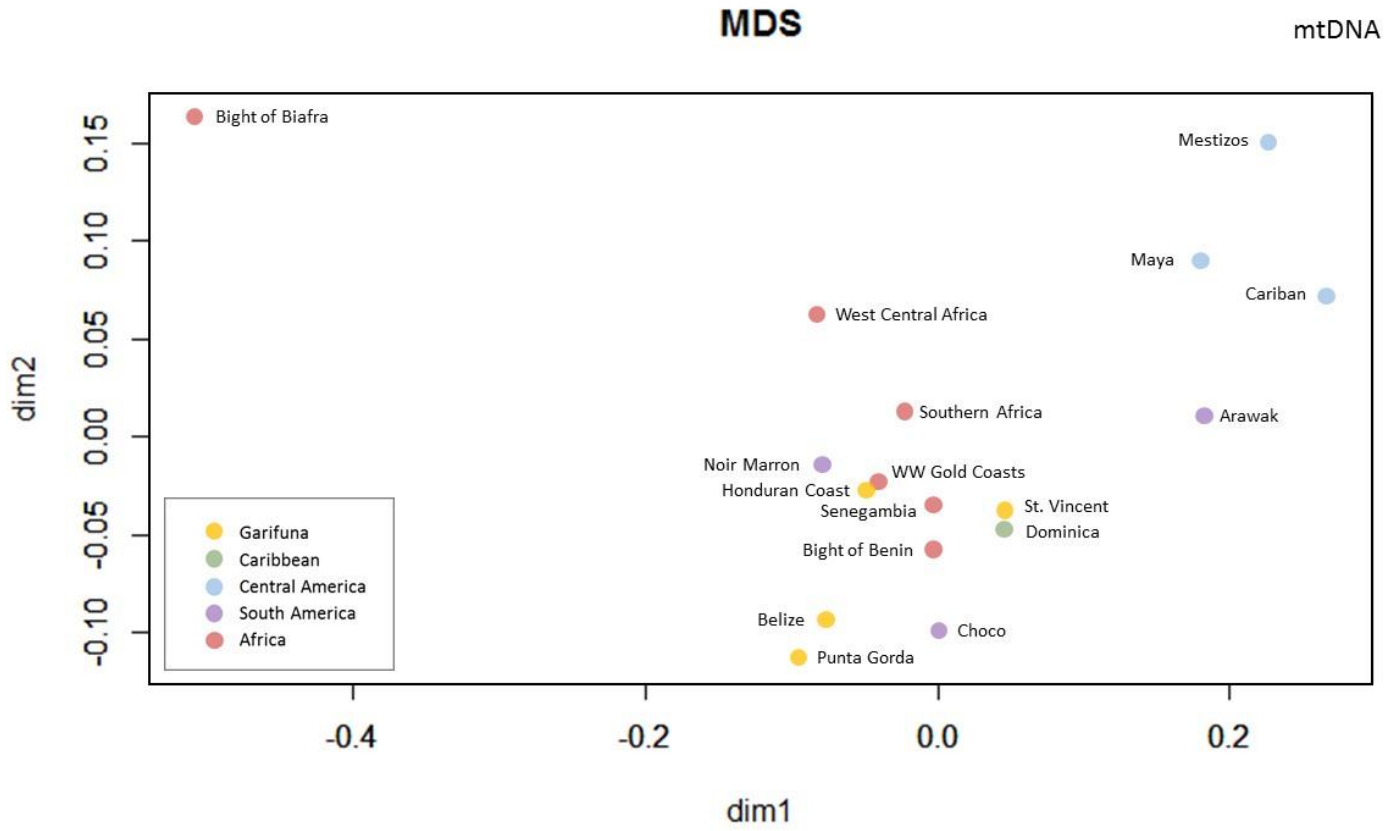

Figure 4.16. MDS plot of Tamura and Nei's genetic distances between Garifuna from St. Vincent, the Honduran Coast, Belize, and Punta Gorda, Roátan, compared to other populations.

Y chromosome results

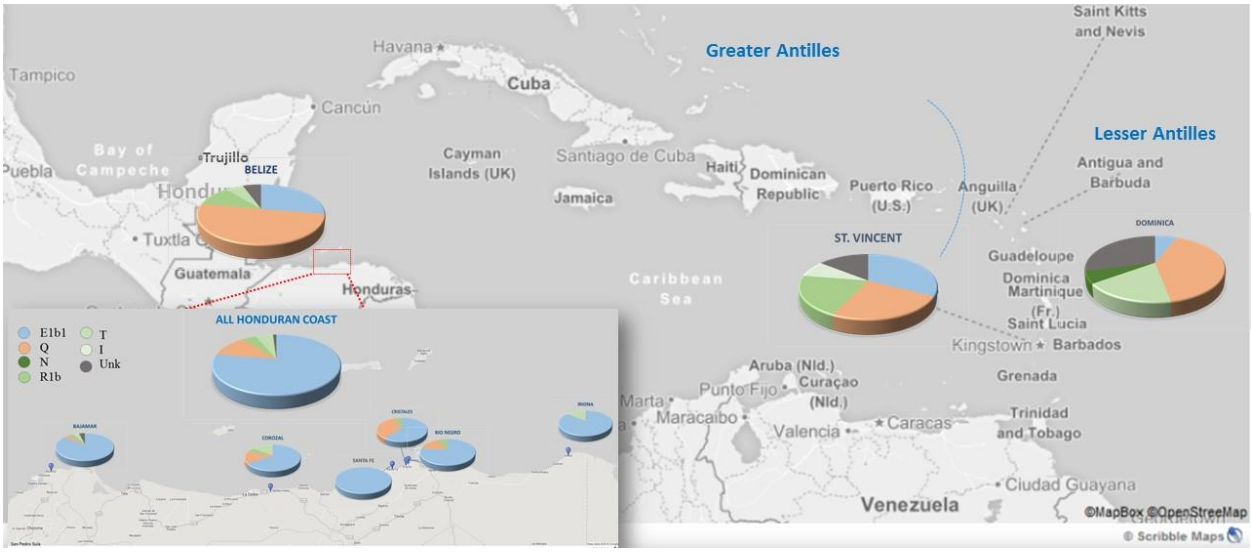

Figure 4.17. Y haplogroups found in 6 Garifuna villages along the Honduran coast, St. Vincent (Phillips-Krawczak, 2012; Benn Torres, et al., 2015), Belize, and the Carib Reserve on Dominica (Phillips-Krawczak, 2012).

Twenty-seven Y-STR haplotypes for the neighborhoods of Rio Negro, Cristales, and Santa Fe are shown in Tables 4.8-4.10. The geographic distribution of these communities and their haplogroup composition compared to the islands in the Lesser Antilles are shown in Figure 4.6. Fifteen male participants provided Y-STR data from the village of Cristáles, each with unique Y-STR haplotypes as shown in Table 4.8. Nine of the 15 (60%) participants had haplotpyes belonging to African haplogroups E1b1, 8 of which belonged to haplogroup E1b1a and the other belonging to E1b1b. Five of the participants (33%) were classified as belonging to Amerind haplogroup Q, and one individual belonged to European haplogroup R1b. In Barrio Rio Negro, 13 individuals Y-STR data, with 11 unique Y-STR haplotypes shown in Table 4.9. Of these individuals, 10 (77%) carried a haplotype assigned to African haplogroup E1b1, 8 (61.5% of all haplotypes) belonging to E1b1a. Two individuals (15.4%) carried haplotypes that belonged to Amerind haplogroup Q. A single haplotype was assigned to European haplogroup

Ht	n	DYS 19	DYS 385	DYS 389I	DYS 389II	DYS 390	DYS 391	DYS 392	DYS 393	DYS 437	DYS 438	DYS 439	DYS 448	DYS 449	DYS 456	DYS 458	DYS 460	DYS 481	DYS 518*	DYS 533	DYS 570	DYS 576	DYS 627*	DYS 635	Y GATA H4	DYF 387 S1*	Haplo-group	Prob
C001	1	16	17,18	13	30	21	10	11	14	14	11	12	21	31	15	17	11	26	41	11	17	16	19	22	11	38,40	**E1b1**	99.8
C002	1	15	16,18	13	30	21	10	10	13	14	11	12	21	29	15	17	10,11	28	38	11	21	16	19	21	11	35,39	**E1b1a**	100
C003	1	15	16,18	13	32	21	10	10	13	14	11	12	21	29	15	17	10	28	38	11	21	16	19	21	12	35,39	**E1b1a**	100
C004	1	16	17	13	30	21	10	11	14	14	10	12	22	33	15	17	11	25	40	11	17	16	20	21	11	39	**E1b1a**	100
C005	1	16	17,18	13	30	21	10	11	14	14	11	12	21	31	15	16	11	26	41	11	17	16	19	22	11	38,40	**E1b1a**	100
C006	1	16	17,18	13	30	21	10	11	14	14	11	12	21	31	15	16	11	26	41	11	18	16	19	22	11	38,40	**E1b1a**	100
C007	1	16	17,20	13	30	21	10	12	15	14	11	12	20	29	15	16	10	25	41	12	17	15	18	21	11	38,39	**E1b1a**	100
C008	1	17	16,17	13	31	21	11	11	14	14	11	10	20	31	15	15	11	25	41	11	17	17	18	24	11	37,38	**E1b1a**	100
C009	1	17	16,18	13	31	21	11	11	14	14	11	10	20	30	15	15	11	26	41	11	17	18	18	23	11	37,38	**E1b1a**	100
C010	1	12	14,19	13	29	24	10	15	13	14	12	12	20	28	15	16	10	24	37	13	17	19	20	23	11	- ,40	**Q**	100
C011	1	13	13	14	31	23	10	13	13	14	10	11	19	28	17	15	10	25	37	12	17	15	21	23	11	34,39	**Q**	99.6
C012	1	13	13,17	14	31	23	10	13	13	14	10	11	19	28	17	15	10	25	37	12	17	15	22	23	11	34,39	**Q**	99.4
C013	1	13	13,17	14	31	23	10	13	13	14	10	11	19	28	17	15	10	25	39	12	17	15	22	23	11	34,39	**Q**	99.4
C014	1	14	13,18	12	29	23	10	14	13	14	11	11	20	29	15	15	10	24	40	11	16	18	20	22	12	36,40	**Q**	99.3
C015	1	14	11,14	14	30	23	11	13	13	15	12	12	19	29	15	15	11	22	37	12	16	16	23	23	12	35,36	**R1b**	100

* Y-STR markers were not used to infer haplogroup in Whit Athey's

Table 4.8. Y chromosome haplotypes and inferred haplogroups found in 15 participants from Barrio Cristáles, on the Honduran coast.

Ht	n	DYS 19	DYS 385	DYS 389I	DYS 389II	DYS 390	DYS 391	DYS 392	DYS 393	DYS 437	DYS 438	DYS 439	DYS 448	DYS 449	DYS 456	DYS 458	DYS 460	DYS 481	DYS 518*	DYS 533	DYS 570	DYS 576	DYS 627*	DYS 635	Y GATA H4	DYF 387 S1*	Haplo-group	Prob
RN01	1	13	13,17	14	31	23	10	12	13	14	10	11	19	28	17	15	11	25	37	12	17	15	21	23	11	34,39	**E1b1**	75.7
RN02	1	16	17,18	13	30	21	10	11	14	14	11	12	21	31	15	17	11	26	41	11	17	16	19	22	11	38,40	**E1b1**	99.8
RN03	2	15	16,17	13	31	21	10	11	13	14	11	12	22	29	15	17	10	28	40	11	18	15	19	21	12	38,39	**E1b1a**	100
RN04	1	15	16,17	13	31	21.1	10	11	13	14	11	12	22	29	15	17	10	28	40	11	18	15	19	21	12	38, -	**E1b1a**	100
RN05	2	16	16,18	13	30	21	10	11	14	14	11	13	21	28	15	16	10	28	38	11	20	15	19	22	12	36,40	**E1b1a**	100
RN06	1	16	19,19	13	-	21	10	11	15	14	11	12	21	29	16	16	10	25	41	11	18	16	17	21	11	37, -	**E1b1a**	100
RN07	1	16	8,18	12	29	21	10	11	14	14	11	12	21	30	17	17	10	26	40	11	17	16	19	21	10	38	**E1b1a**	100
RN08	1	18	16,17	13	31	21	11	11	14	14	11	10	20	30	15	15	11	26	41	11	17	17	18	25	11	37,38	**E1b1a**	100
RN09	1	12	14,18	13	29	24	10	15	13	14	12	12	20	28	15	16	10	24	37	13	17	19	21	23	11	- ,40	**Q**	92.6
RN10	1	14	13,18	12	29	24	10	14	13	14	11	11	20	29	15	15	10	24	40	11	16	18	20	22	12	35,39	**Q**	99.9
RN11	1	14	11	13	28	23	11	13	13	15	12	11	20	28	15	17	11	22	36	12	17	17	22	23	13	35,36	**R1b**	100

* Y-STR markers were not used to infer haplogroup in Whit Athey's

Table 4.9. Y chromosome haplotypes and inferred haplogroups found in 13 participants from Barrio Rio Negro, on the Honduran coast.

Ht	n	DYS 19	DYS 385	DYS 389I	DYS 389II	DYS 390	DYS 391	DYS 392	DYS 393	DYS 437	DYS 438	DYS 439	DYS 448	DYS 449	DYS 456	DYS 458	DYS 460	DYS 481	DYS 518*	DYS 533	DYS 570	DYS 576	DYS 627*	DYS 635	Y GATA H4	DYF 387 S1*	Haplo-group	Prob
SF01	1	14	15,17	13	30	21	10	11	13	14	11	11	21	31	15	17	11	26	37	11	17	16	20	22	12	38,40	**E1b1a**	100
SF02	1	14	15,17	13	30	21	10	11	13	14	11	11	21	28	14	16	10	26	37	11	20	16	20	22	12	37,38	**E1b1a**	100
SF03	1	14	16,17	13	30	21	10	11	13	15	11	11	21	28	14	16	10	26	38	11	20	16	20	21	12	37,38	**E1b1a**	100
SF04	1	15	16,17	13	31	21	10	11	13	14	11	12	22	29	15	17	10	28	40	11	18	15	20	21	12	38,39	**E1b1a**	100
SF05	2	16	17,18	13	30	21	10	11	14	14	11	12	21	31	15	16	11	26	41	11	17	16	19	22	11	38,39	**E1b1a**	100
SF06	1	16	17,19	13	30	21	10	11	14	14	10	12	22	33	15	17	11	25	40	11	17	16	20	21	11	39	**E1b1a**	100
SF07	1	16	18,20	13	30	21	10	12	15	14	11	11	20	29	15	16	10	25	41	12	17	15	18	21	11	38,39	**E1b1a**	100
SF08	4	16	18,20	13	30	21	10	12	15	14	11	12	20	29	15	16	10	25	41	12	17	15	18	21	11	38,39	**E1b1a**	100
SF09	2	17	17	13	31	21	11	11	14	14	11	10	20	30	15	15	11	26	41	11	17	17	18	24	11	37,38	**E1b1a**	100

* Y-STR markers were not used to infer haplogroup in Whit Athey's

Table 4.10. Y chromosome haplotypes and inferred haplogroups found in 14 participants from Santa Fe, on the Honduran coast.

R1b. Fourteen samples were characterized for Y-STR haplotypes from the village of Santa Fe, yielding a total of 9 haplotypes shown in Table 4.10. Two haplotypes were shared by two individuals and another haplotype was found in four members of the community. All samples from this village were assigned to Y-chromosome haplogroup E1b1a.

Cristales, Rio Negro and Santa Fe were further examined (Figure 4.20). Diversity at each loci was plotted in Figure 4.20a. Santa Fe has the smallest number of alleles at each loci, while Rio Negro has the highest number of alleles at each loci. The lowest diversity at each loci in all three communities was seen in DYS392, DYS449, and DYS458, while the largest diversity in all samples was seen at DYS19, DYS385a/b, and DYS448. Expected heterozygosity at each of the 27 loci showed that Santa Fe had the lowest expected diversity at most loci, with Rio Negro and Cristales varying depending on the loci examined (Figure 4.20b). A matrix of Reynold's coancestry coefficients can be viewed in Figure 4.20c. This measure shows that Cristales and Rio Negro have the shortest divergence times, while Cristales and Santa Fe have the longest divergence times from each other. The final graph, Figure 4.20d, shows that the variation within Cristales and Rio Negro is high, whereas Santa Fe has little diversity variation. The amount of variation between Cristales and Rio Negro, as well as Nei's mean number of pairwise differences between pairs of populations is relatively high, while the same measures between Cristales and Santa Fe are low.

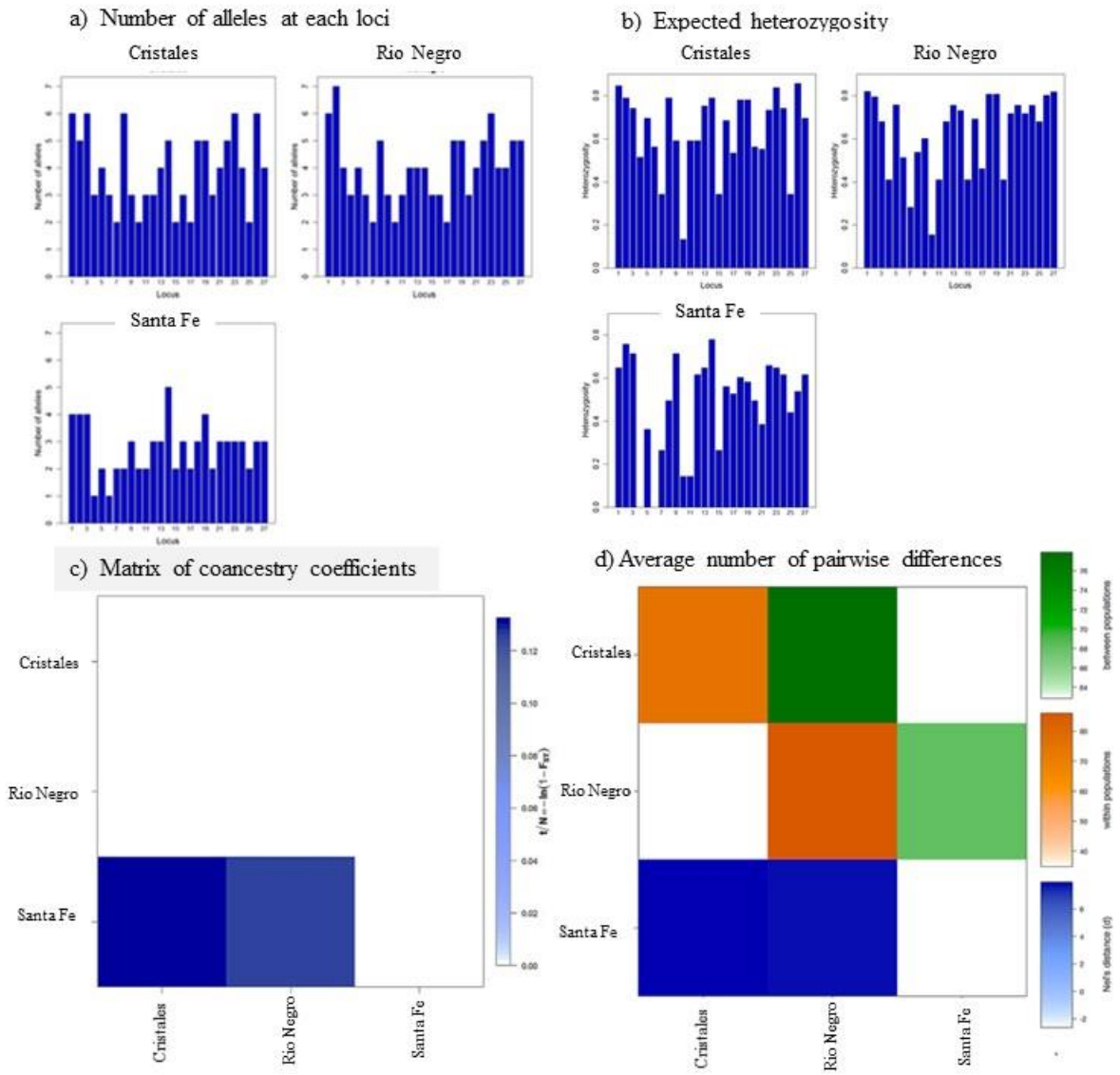

Figure 4.18. Analyses of 27 loci in 3 Garifuna Villages: a) number of alleles at different loci; b) expected heterozygosity at each loci; c) Reynold's coancestry coefficient; d) average number of pairwise differences within villages (orange), between populations (green), and net number of nucleotide differences between populations (blue).

The data provided by Dr. Matamoros is presented in Table 4.12. Haplogroup assignments for all villages are shown in Table 4.11. In Corozal, 20 individuals were typed for 11 Y-STRs, with 13 individuals assigned to haplogroup E1b1a (65%), 3 assigned to haplogroup Q (15%), 3 individuals assigned to haplogroup T (15%), and one individual was assigned to haplogroup R1b (5%). Only 7 individuals were typed from Iriona, with 6 individuals assigned to haplogroup E1b1a (86%) and 1 individual assigned to haplogroup T. The sample from Bajamar consisted of 25 individuals. Nearly all (21 samples, 84%) were assigned to haplogroup E1b1a, with 1 sample each of haplogroups Q, R1b, T (each making up 4% of the sample), and a haplotype that could not be assigned to a haplogroup by the haplogroup predictor program (Table 4.11).

Table 4.11. Haplogroups identified in Garifuna and Carib populations in Central America and the Caribbean.

Haplgroup	Dominica[1]	St. Vincent[1]	St. Vincent[2]	St. Vincent Total	Cristales	Rio Negro	Santa Fe	Bajamar	Iriona	Corozal	Honduran Coast Total	Belize[1]
E1b1		8 (25%)	12 (48%)	20 (35%)	1 (7%)	2 (15%)					23 (24%)	5 (28%)
E1b1a	1 (6%)				8 (53%)	8 (62%)	14(100%)	21 (84%)	6(86%)	13 (65%)	50 (53%)	
Q	7 (41%)	9 (28%)	3 (12%)	12 (21%)	5 (33%)	2 (15%)		1 (4%)		3 (15%)	11(12%)	9 (50%)
R1a		1 (3%)		1 (2%)								1 (6%)
R1b		6 (19%)	7 (28%)	13 (23%)	1 (7%)	1 (8%)		1 (4%)		1(5%)	4 (4%)	1 (6%)
T	3 (18%)							1 (4%)	1 (14%)	3 (15%)	5 (5%)	1 (6%)
I1			2 (8%)	2 (4%)								
I2a		1 (3%)		1 (2%)								
I2b			1 (4%)	1 (2%)								
N	1 (6%)											
Unknown	5 (29%)	7 (22%)		7 (12%)				1 (4%)			1 (1%)	1 (6%)
Total	**17**	**32**	**25**	**57**	**15**	**13**	**14**	**25**	**7**	**20**	**94**	**18**

[1]Phillips-Krawzack 2012; [2]Benn Torres et al. 2015

Table 4.12. Y-STR haplotypes and inferred haplogroups from Corozal (Cor), Iriona (Iri) and Bajamar (Baj).

Ht	n	DYS19	DYS385	DYS 389I	DYS 389II	DYS390	DYS391	DYS392	DYS393	DYS437	DYS438	DYS439	Haplo-group	Prob
1Cor	1	15	16,17	13	30	20	10	11	14	13	11	12	E1b1a	100
2Cor	1	15	18,20	13	30	21	10	12	15	14	11	12	E1b1a	100
3Cor	1	16	16,18	13	30	21	10	10	13	14	11	12	E1b1a	100
4Cor	1	16	17,18	13	30	21	10	11	15	14	11	12	E1b1a	100
5Cor	4	16	18,20	13	30	21	10	12	15	14	11	12	E1b1a	100
6Cor	2	15	16,18	13	31	21	10	10	13	14	11	12	E1b1a	100
7Cor	1	17	18,18	13	29	21	10	11	15	14	11	14	E1b1a	100
8Cor	1	17	16,17	13	31	21	11	11	14	14	11	10	E1b1a	100
9Cor	1	17	17	13	31	21	11	11	14	14	11	10	E1b1a	100
10Cor	1	13	14	12	29	24	10	15	12	14	11	13	Q	100
11Cor	1	12	15,19	13	29	24	10	15	13	14	11	11	Q	99.9
12Cor	1	12	15	13	29	24	10	15	13	14	11	12	Q	99.7
13Cor	1	14	11,16	13	29	25	10	13	13	14	12	12	R1b	99.2
14Cor	1	13	14,17	14	30	23	10	13	13	14	10	11	T	96
15Cor	2	13	13,17	14	31	23	10	13	13	14	10	11	T	96
1Iri	3	16	18,20	13	30	21	10	12	15	14	11	12	E1b1a	100
2Iri	1	16	18,21	13	30	21	10	12	15	14	11	12	E1b1a	100
3Iri	1	15	16,18	13	31	21	10	10	13	14	11	12	E1b1a	100
4Iri	1	15	16,17	13	31	21	10	11	13	14	11	12	E1b1a	100
5Iri	1	13	13,17	14	31	23	10	13	13	14	10	11	T	88.6
1Baj	2	14	15,17	13	30	21	10	11	13	14	11	11	E1b1a	97.3
2Baj	1	15	17,19	13	29	21	10	11	14	14	11	12	E1b1a	100
3Baj	1	15	16,17	13	30	20	10	11	14	13	11	12	E1b1a	100
4Baj	2	16	18,20	13	30	21	10	12	15	14	11	12	E1b1a	100
5Baj	1	17	17,18	13	30	21	10	11	14	14	11	12	E1b1a	100
6Baj	6	15	16,18	13	31	21	10	10	13	14	11	12	E1b1a	100
7Baj	4	15	16,17	13	31	21	10	11	13	14	11	12	E1b1a	100
8Baj	1	15	15,18	13	31	21	10	10	13	14	11	13	E1b1a	100
9Baj	1	15	15,18	14	31	21	10	11	14	14	11	13	E1b1a	100
10Baj	1	15	16,18	14	32	21	10	10	13	14	11	13	E1b1a	100
11Baj	1	16	17	13	31	21	11	11	14	14	11	10	E1b1a	100
12Baj	1	17	16,18	13	31	21	11	11	14	14	11	11	E1b1a	100
13Baj	1	12	14,19	13	29	24	10	15	13	14	12	12	Q	100
14Baj	1	14	11,14	13	29	24	11	13	14	15	12	12	R1b	100
15Baj	1	13	13,17	14	31	23	10	13	13	14	10	11	T	88.6
16Baj	1	16	13	12	30	22	10	12	12	17	10	11	Unk	na

Summary statistics for all Garifuna communities, and all comparative populations are shown in Table 4.13. When all 27 loci are included in the analyses, Cristales has the highest diversity measures (H = 1, π = 16.32, π_n = 0.63) and Santa Fe (H = 0.9231, π = 13.22, π_n = 0.49) has the lowest. However, when diversity is calculated using 10 loci, Rio Negro has the highest gene diversity (0.9487), while Cristales retains the highest average number of pairwise differences (5.66). Using 10 loci haplotypes, all of the Garifuna communities on the Honduran coast had a lower gene diversity measures (H = 0.9536, π = 5.11, π_n = 0.52) than those seen in

the Garifuna on St. Vincent Island (H = 0.9964, π = 5.70, π_n = 0.63). Of the coastal communities, Corozal had the highest gene diversity (0.9526) and expected diversity (18.47). Cristales had the highest average pairwise differences between haplotypes (5.66) and average diversity of loci (0.32). The community of Iriona had the lowest measures of diversity compared to all other coastal populations (H = 0.7143, π = 3.67, π_n = 0.37). The Garifuna communities had a lower a gene diversity than populations from Central America, the Caribbean Islands, Europe, Africa and most of South America, except for the Tupi (0.6957), Arawak (0.9605) and Cariban Speakers(0.9427). The average number of differences, however, were similar or higher than many of populations, as the Garifuna are composed of several haplotypes that come from multiple geographic locations.

Median joining networks were constructed for haplogroups E1b1 and Q for Cristales, Rio Negro and Santa Fe using 19 loci (Figure 4.21). In the network for E1b1, more similarities are seen between haplotypes belonging to Cristales and Santa Fe, and the communities have two haplotypes shared between them. Several haplotypes from Cristales and Santa Fe have a 1 or 2 repeats difference between them, indicating a close relationship. The Rio Negro haplotypes are more dispersed throughout the network, have the most divergent haplotypes, and show little relation to one another. Figure 4.21 also shows a median joining network of haplotypes belonging to haplogroup Q from Rio Negro and Cristales. There were no Native American haplotypes found in the sample from Santa Fe. In total, there are seven haplotypes that make up 4 nodes on the network. Two nodes containing haplotypes from Rio Negro and Cristales are a single repeat difference from one another. One node is shared by Rio Negro and Cristales. The final node in the network, which is several mutations away from the other nodes in the network, is made up of 3 Q haplotypes from Cristales.

Table 4.13. Summary statistics for Y-STR data from Garifuna communities, neighboring groups, and possible source populations.

*	Population	n	# ht	loci	H	+/-	π	+/-	π_n	+/-	ϑ_H	S.D. ϑ_H
Garifuna	**Cristales**	**15**	**15**	**27**	**1.0000**	**0.02**	**16.32**	**7.71**	**0.63**	**0.33**	**na**	**na**
		15	10	10	0.9333	0.04	5.66	2.87	0.57	0.32	12.50	9.80
	Rio Negro	**13**	**11**	**27**	**0.9744**	**0.04**	**14.59**	**6.99**	**0.61**	**0.33**	**36.20**	**58.91**
		13	10	10	0.9487	0.05	4.41	2.37	0.49	0.29	16.89	18.88
	Santa Fe	**14**	**10**	**27**	**0.9231**	**0.06**	**13.22**	**6.33**	**0.49**	**0.26**	**10.56**	**9.82**
		14	8	10	0.9011	0.06	3.38	1.84	0.34	0.21	7.81	5.55
	Total (27 loci)	**119**	**62**	**27**	**0.9643**	**0.01**	**5.18**	**2.52**	**0.52**	**0.28**	**25.25**	**6.09**
	Corozal	20	14	10	0.9526	0.03	5.26	2.65	0.53	0.3	18.47	14.30
	Iriona	7	4	10	0.7143	0.18	3.67	2.11	0.37	0.24	1.92	1.79
	Bajamar	26	16	10	0.9292	0.03	4.40	2.24	0.44	0.25	11.66	6.70
	St. Vincent	24	23	10	0.9964	0.01	5.70	2.83	0.63	0.35	273.03	1014.23
	Total	**120**	**49**	**10**	**0.9536**	**0.01**	**5.11**	**2.50**	**0.52**	**0.28**	**18.93**	**3.87**
Central America	Cent Amer Mestizos	279	195	10	0.9931	0.00	6.28	2.99	0.63	0.33	142.30	39.66
	Cent Amer Gen Pop	535	320	10	0.9935	0.00	6.34	3.01	0.63	0.33	151.65	28.94
	Mayan	99	53	10	0.9709	0.01	4.70	2.32	0.47	0.26	31.63	8.00
	Honduras	128	109	10	0.9972	0.00	6.14	2.94	0.61	0.33	350.41	184.04
	Belize	157	132	10	0.9975	0.00	6.19	2.96	0.62	0.33	392.05	173.71
	Costa Rica	124	98	10	0.9915	0.00	6.68	3.17	0.67	0.35	114.39	48.83
	Total (-Arawak/Cariban)	**937**	**649**	**10**	**0.9980**	**0.00**	**6.32**	**3**	**0.63**	**0.33**	**509.30**	**80.22**
Caribbean Islands	Bahamas	426	269	10	0.9964	0.00	5.86	2.01	0.59	0.31	272.18	43.03
	Haiti	123	116	10	0.9991	0.00	5.83	2.8	0.58	0.31	1068.86	1364.70
	Jamaica	194	162	10	0.9965	0.00	5.93	2.84	0.59	0.31	285.04	111.49
	Dominica	21	16	10	0.9714	0.02	5.64	2.82	0.56	0.31	32.22	28.48
	Grenada	35	32	10	0.9933	0.01	5.77	2.83	0.58	0.31	145.80	207.98
	St. Lucia	24	23	10	0.9964	0.01	6.61	3.24	0.66	0.36	273.03	1014.23
	St. Kitts	33	30	10	0.9886	0.01	5.15	2.58	0.51	0.28	85.09	103.33
	St. Vincent	21	18	10	0.9857	0.02	5.99	2.97	0.60	0.33	67.11	92.49
	Puerto Rico	121	101	10	0.9956	0.00	6.39	3.05	0.64	0.34	223.91	105.02
	Trinidad	36	34	10	0.9968	0.01	5.76	2.82	0.58	0.31	312.03	740.51
	St. Thomas	134	107	10	0.9955	0.00	5.52	2.67	0.55	0.3	219.81	84.51
	Afro-Caribbean	**1164**	**456**	**10**	**0.9898**	**0.00**	**5.97**	**2.85**	**0.60**	**0.31**	**94.65**	**8.69**
	First People, Trinidad	**5**	**4**	**9**	**0.9**	**0.16**	**4.50**	**2.66**	**0.50**	**0.35**	**7.01**	**15.16**
	Total	**1169**	**714**	**10**	**0.9976**	**0.00**	**5.98**	**2.85**	**0.60**	**0.32**	**413.60**	**45.87**
South America	South America	173	120	10	0.9899	0.00	6.02	2.88	0.60	0.32	96.27	27.77
	Tupi Speakers	42	7	10	0.6957	0.06	3.97	2.03	0.40	0.23	1.75	0.51
	Noir Marron	42	23	10	0.957	0.02	4.81	2.40	0.48	0.27	20.60	8.04
	Mestizos	305	202	9	0.9901	0.00	5.68	2.73	0.63	0.34	98.52	24.21
	Arawak Speakers	144	52	10	0.9605	0.01	4.52	2.24	0.50	0.28	22.60	4.66
	Cariban Speakers	99	37	10	0.9427	0.01	5.05	2.47	0.51	0.27	14.88	3.26
	Windward Coast	90	60	10	0.9860	0.00	3.94	1.99	0.39	0.22	68.63	22.62
Africa	West Central Africa	174	112	10	0.9888	0.00	4.53	2.24	0.45	0.25	86.15	21.82
	Bight of Benin	297	185	10	0.9937	0.00	4.56	2.25	0.46	0.25	154.60	29.16
	Bight of Biafra	12	12	10	1.0000	0.03	3.65	1.99	0.37	0.22	na	na
	Senegambia	205	178	10	0.9984	0.00	5.51	2.66	0.55	0.29	312.01	272.54
	Southern Africa	405	242	10	0.9944	0.00	5.46	2.64	0.55	0.29	175.06	27.45
	Madagascar	110	71	10	0.9860	0.00	5.28	2.57	0.53	0.28	68.48	20.93
	Total	**1293**	**713**	**10**	**0.9968**	**0.00**	**5.20**	**2.52**	**0.52**	**0.28**	**309.16**	**28.15**
Europe	United Kingdom	1269	712	10	0.9920	0.00	4.78	2.34	0.48	0.26	122.50	13.67
	France	76	66	10	0.9954	0.00	5.74	2.78	0.57	0.31	216.27	159.01
	Portugal	23	21	10	0.9921	0.02	3.60	1.90	0.36	0.21	123.56	245.98
	Spain	393	295	10	0.9963	0.00	4.87	2.38	0.49	0.26	265.42	61.07
	Total	**1761**	**994**	**10**	**0.9942**	**0.00**	**4.92**	**2.40**	**0.49**	**0.27**	**170.49**	**16.83**

* Sample size (n), Number of halpotypes (# ht), Number of loci (loci), Gene diversity (H), mean number of pairwise differences (π), average diversity of loci (π_n), Theta Hom (θ_H).

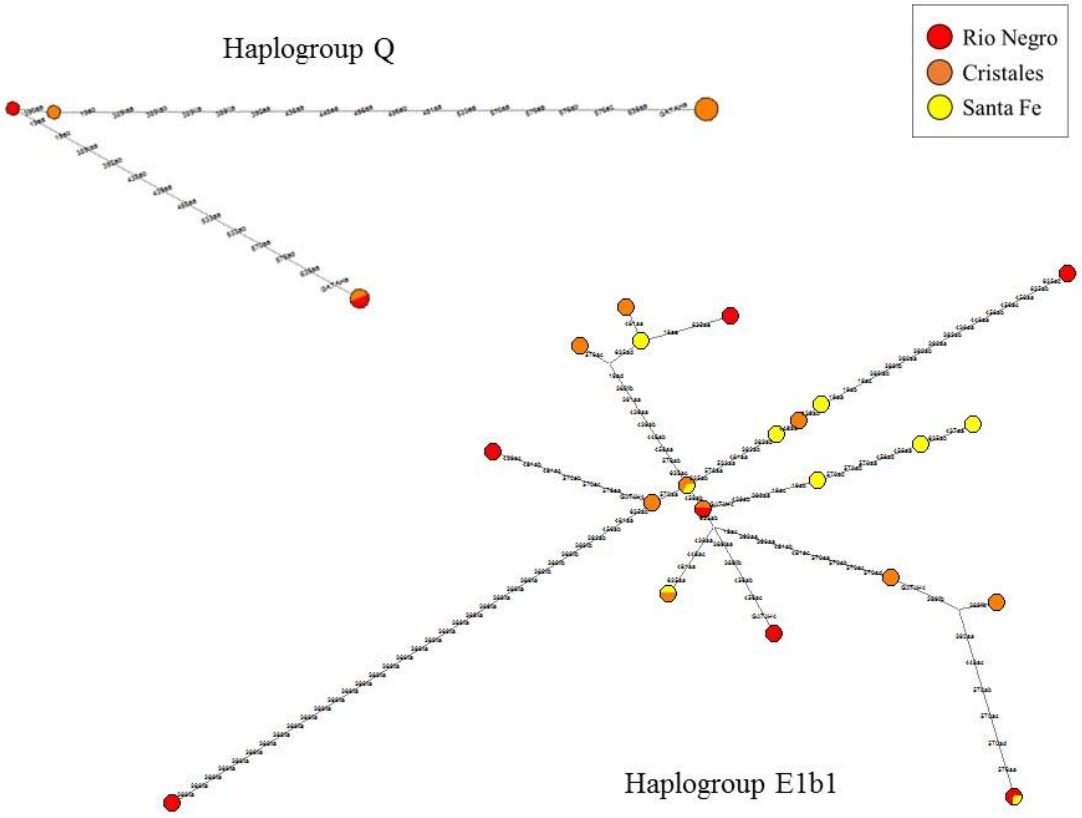

Figure 4.19. Network of 19 Y-STR E1b1 haplotypes from Rio Negro (n=10), Cristales (n=9), and Santa Fe (n=14, and Q haplotypes from Rio Negro (n=2) and Cristales (n=5).

Q and E1b1 Networks were also constructed to include the 10 loci Y-STR haplotypes from the Garifuna villages of Corozal, Bajamar, and Iriona (Figure 4.22). The haplotypes belonging to haplogroup Q show several haplotypes that are generally multiple mutational steps apart from one another. There are 3 haplotypes that are 1 to 2 mutational steps away, 2 that are found in 1 individual from Corozal, and another that is shared by three individuals from Corozal, Cristales, and Rio Negro. Two other nodes represent haplotypes a single step away from one another in Cristales and Rio Negro. One distantly related node is shared by two individuals from Cristales and an individual from Bajamar. The larger network includes most of the haplotypes in

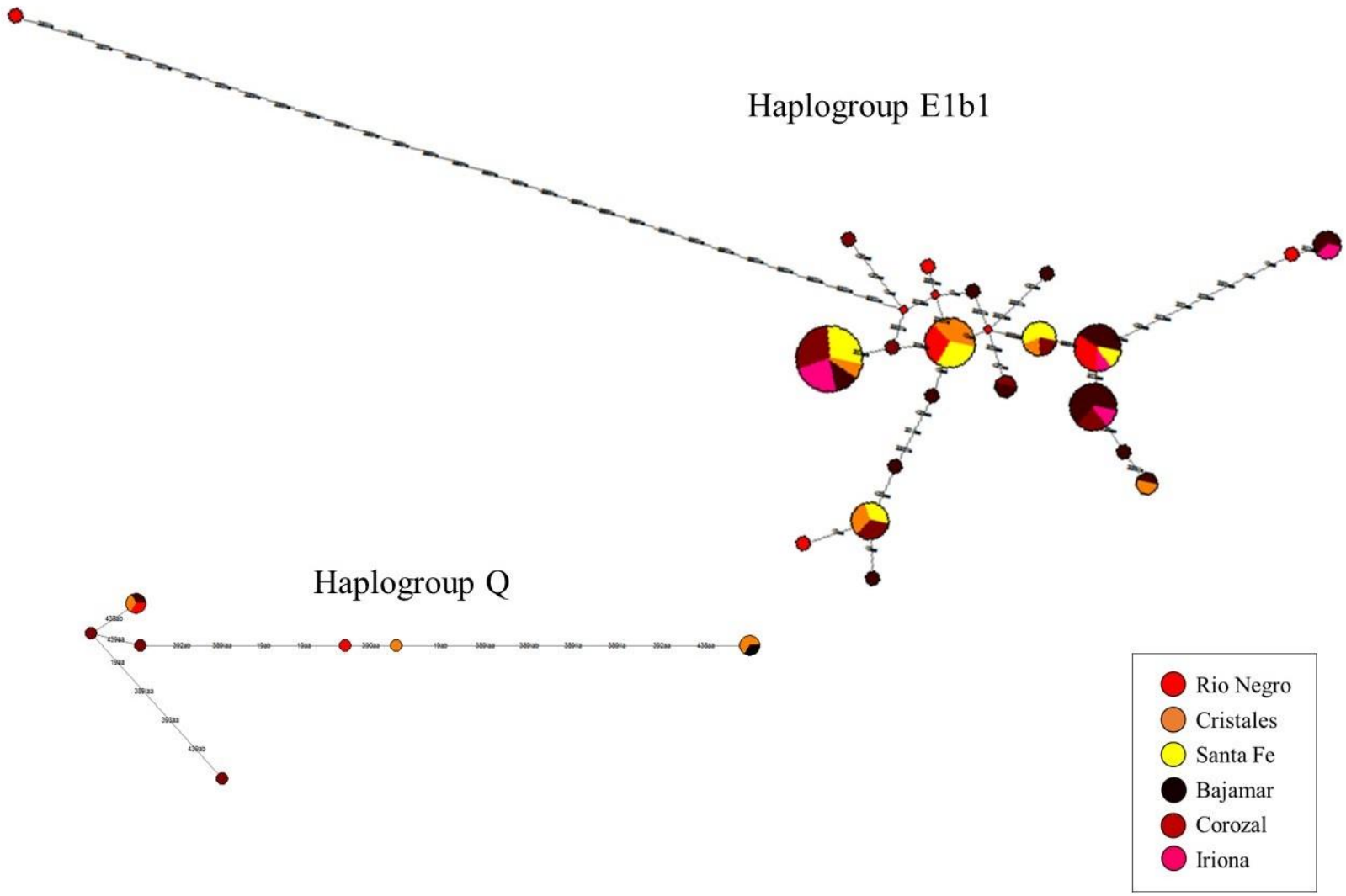

Figure 4.20. Median joining network of 10 loci E1b1 haplotypes from 6 Garifuna villages on the Honduran coast, Rio Negro (n=10), Cristales (n=9), Santa Fe (n=14), Bajamar (n=21), Corozal (n=13), Iriona (n=6) and Q haplotypes from 4 Garifuna villages on the Honduran coast, Rio Negro (n=2), Cristales (n=5), Bajamar (n=1), Corozal (n=3).

the 6 villages that belong to the African haplogroup E1b1, and many haplotypes are shared between villages. The node that displays the largest number of samples represents a haplotype shared by all villages except for Rio Negro. Two smaller nodes are shared between Santa Fe, Cristales, and Corozal; another node is shared between Rio Negro, Cristales, and Santa Fe. Two large nodes are shared between Rio Negro, Bajamar and Santa Fe, and Bajamar, Corozal and Iriona. Most of the haplotypes form a cluster with only a few mutational steps different. However, two haplotypes from Rio Negro, and a node shared by Iriona and Bajamar are not closely related to the other haplotypes in the figure.

An MDS plot of Slatkin's linearized FST distances was constructed to better visualize the relationship between the six coastal Garifuna villages and the Garifuna of Kingstown, St. Vincent (Benn Torres, et al., 2015). The St. Vincent population, with the highest frequency of European and Native American haplotypes, is on the far right side of the plot. Santa Fe, a community where all of the Y-STR haplotypes were of African origin and belonged to haplogroup E1b1a, plotted on the farthest left of the plot. Excluding Santa Fe, the central villages included in the plot, Corozal, Cristales, and Rio Negro, plotted closely together in the center of the plot. Bajamar, a village with mostly African haplotypes, but also includes haplotypes belonging to European haplogroups R1b and T and Native American haplogroup Q, plots in the lower center of the plot. Iriona, with no Native American lineages, and a high frequency of haplogroup T plots towards the lower left portion part of the plot Figure 4.23.

Intrapopulation measure for Garifuna and geographical regions that were contributors to the Garifuna gene pool, or share a similar history, are shown in Figure 4.24. Nei's net pairwise distances, within population pairwise differences, and the average pairwise differences between populations were graphed in 4.24a. The Garifuna have the lowest level of within population

differences, are most similar to other Afro-Caribbean populations based on Nei's net pairwise distances and the average number of differences between populations. European populations show the least relationship to all groups included. Figure 4.24b and Figure 4.24c, Reynold's coancestry coefficient time of divergence between populations, show that the Garifuna and Afro-Caribbean populations share a similar ancestry and time of divergence with African groups. Figure 4.24d shows the allelic size range at different loci between the 6 groups. The Garifuna, a population that historically has gone through several episodes of bottlenecks, show the smallest range in allele size in all loci. Admixed groups from Central America, the Caribbean and South America show slightly larger allelic size ranges, and Africa and Europe show the largest allelic size ranges.

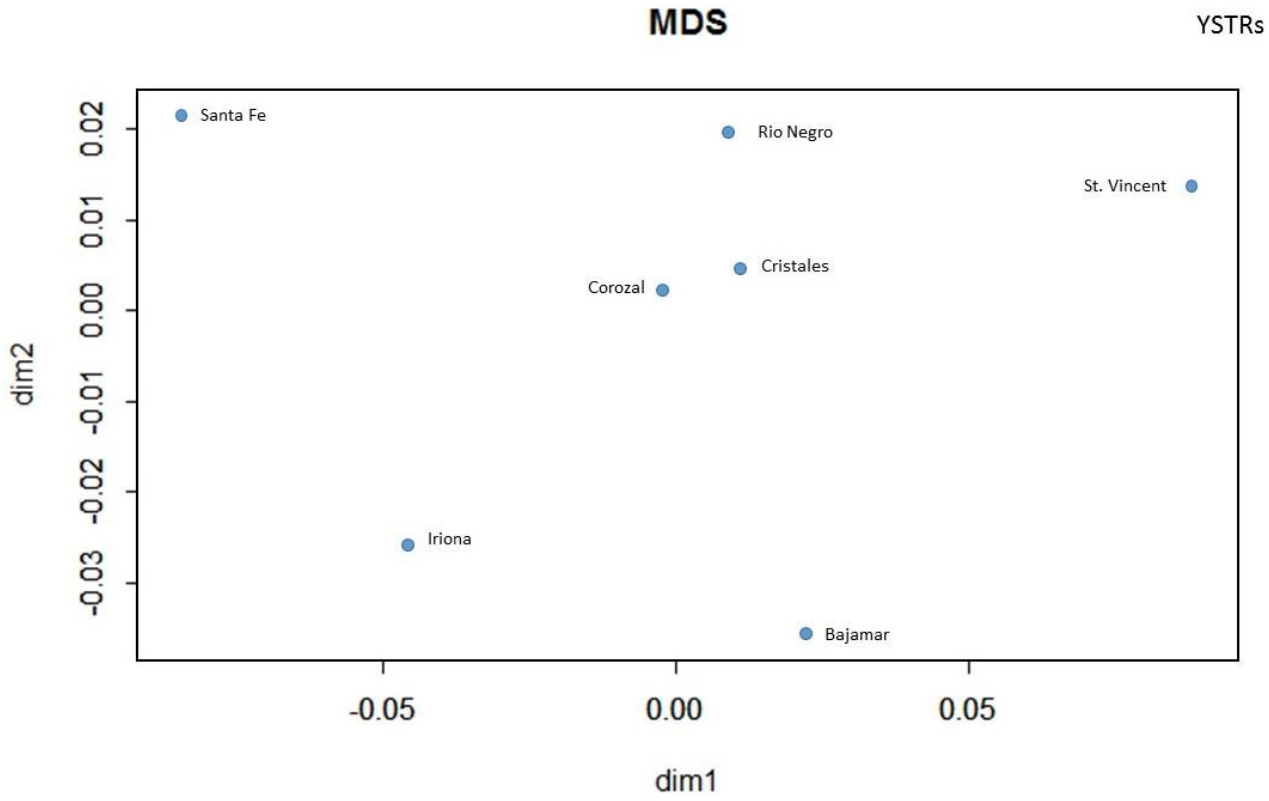

Figure 4.21. MDS plot of Slatkin's linearized FST distances between Garifuna villages.

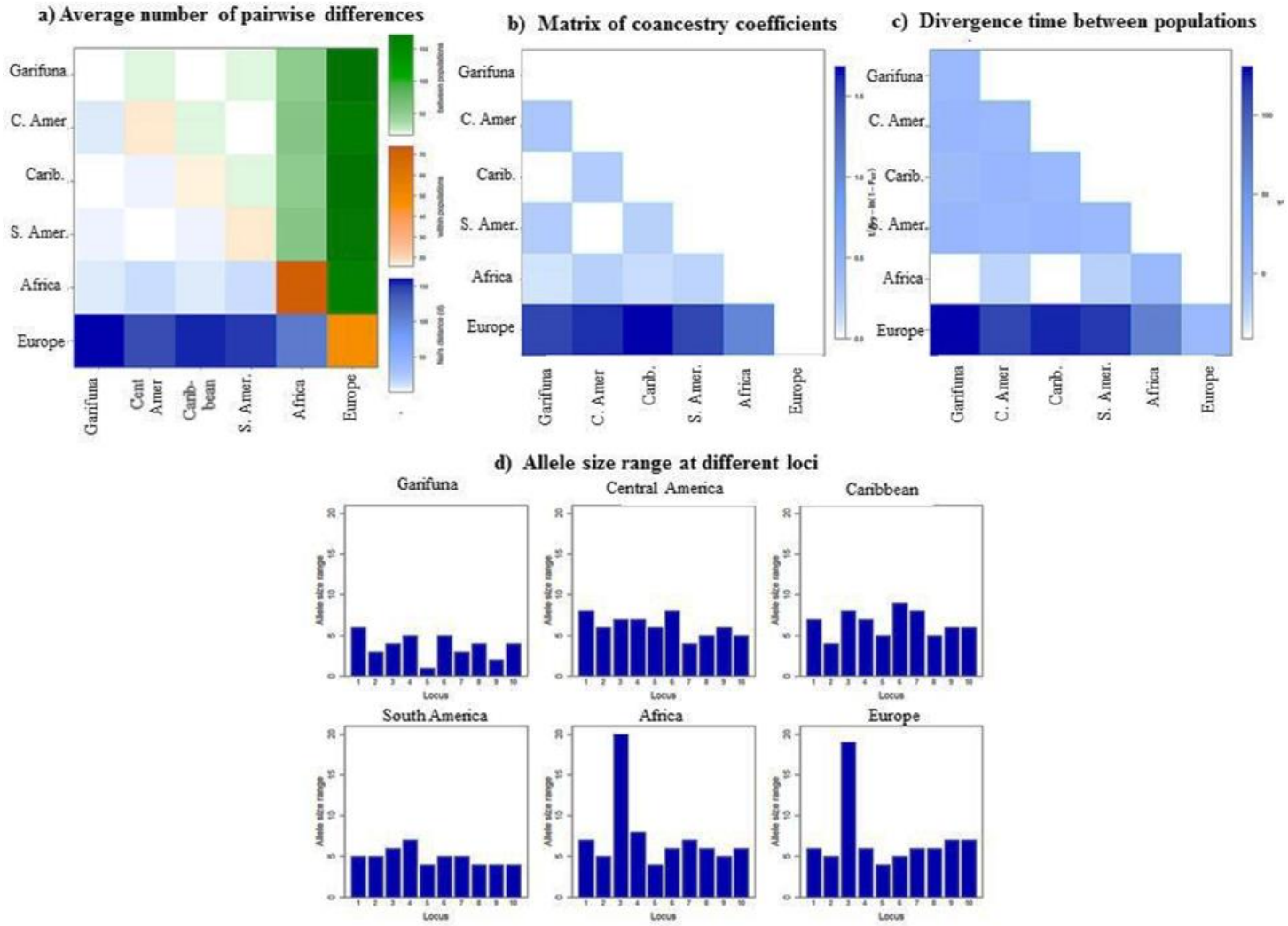

Figure 4.22. Intrapopulation measures between Garifuna and geographic regions including Central America, the Caribbean Islands, South America, Africa and Europe: a) average number of pairwise differences within populations (orange), between populations (green), and net number of nucleotide differences between populations (blue); b) Reynold's coancestry coefficient; c) divergence time between populations; and d) allele size range at 10 loci in all groups.

Analysis of molecular variance was calculated to examine the genetic structure of the populations by geography (Table 4.14), and by known admixture (Table 4.15). The AMOVA based on geographic groupings (Garifuna, Central America, Caribbean Islands, South America, Africa and Europe) showed that the majority (61.33%) of genetic variation could be explained among the geographic groups, and 23.1 percent could be explained by variation within the populations (Table 4.14). The groupings that combined groups with similar admixture components (Garifuna, European and Amerindian admixed Mestizos and the general population from Central and South America, groups with African ancestry in the Caribbean and South America including the Choco and the Noir Marron, Amerindian groups, and African populations) showed a different picture, with only 28.97 percent of the variation explained by variation among the groups, and 67.75 percent of the variation explained by variation within populations (Table 4.15). These indicate that for Y-STR data, geography can better explain Y variation.

Table 4.14. AMOVA results for Y-STR data by geographic groupings. Groups included Garifuna, Central America, Caribbean Islands, South America, Africa, and Europe.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation
Among Groups	5	171121.703	3.639374 Va	61.33
Among pops. w/in groups	31	35185.632	9.24084 Vb	15.57
Within populations	5581	76509.354	13.70890 Vc	23.1
Total	5617	282816.69	59.34347	

*All values significant at p=0.000 +/-0.000

Table 4.15. AMOVA results for Y-STR data by admixture groupings. Groups included Garifuna, European and Amerindian admixed populations from Central and South America, groups with African ancestry in the Caribbean and South America, Amerindian groups, and Africans.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation
Among Groups	4	8942.48	2.46578 Va	28.97
Among pops. w/in groups	20	911.287	0.27915 Vb	3.28
Within populations	4791	27632.146	5.76751 Vc	67.75
Total	4815	37485.913	8.51245	

*All values significant at p=0.000 +/-0.000

A network was constructed that included all E1b1 haplotypes found in Central and South America, the Caribbean, and Africa (Appendix C.1). Because of the number of haplotypes included, a separate network of E1b1 haplotypes was constructed to include African groups from areas where the slave trade had hosted some of the major ports, including Senegambia, the Windward (and Gold) Coast, Bight of Benin, Bight of Biafra, West Central Africa, Southern Africa and Madagascar (Figure 4.25). Most of the haplotypes were in a center cluster of nodes, which is difficult to unravel. However, of those haplotypes, the most frequent haplotype sharing was with Africans from the Bight of Benin and the Bight of Biafra, though West Central Africa and Southern African haplotypes were also found in high frequency in the comparative literature (Table 4.16). All villages shared nodes with populations from all other African regions, including haplotypes reported from Madagascar. However, two nodes form a branch with Senegambia, where several haplotypes form distinct clusters away from the main cluster of

nodes. A single Garifuna haplotype formed a distance branch off of a cluster of E1b1 haplotypes from Bight of Biafra and Southern Africa. Table 4.16 also showed that many E1b1 haplotypes are shared between Garifuna villages, and are also found in African admixed populations in Central and South America, and especially in African admixed populations throughout the Caribbean.

Networks were also constructed to visualize the relationship between Garifuna and other populations that had native haplotypes belonging to Y haplogroup Q (Appendix C.2). To better examine the relationship between Garifuna and Arawak and Cariban speakers from South America a separate network was constructed (Figure 4.26). All of the Garifuna haplotypes are found in one large branch of the Network that has a mix of haplotypes from Cariban and Arawak speakers throughout it. Only one haplotype shares a node with the South American groups, and it is a haplotype from St. Vincent, shared with Cariban speakers. A small group of haplotypes from Cristales, Corozal, St. Vincent, and Cristales form a side branch with an Arawak Speaker's haplotype. Three haplotypes from Cristales and a haplotype from St. Vincent form another side branch with Arawak haplotypes. A single haplotype from Corozal forms a side branch with a Cariban speaker's haplotype.

To better understand the relationship between the Q haplotypes found in St. Vincent and in Garifuna on the coast, an MDS plot was constructed that included all the Q haplotypes found in the literature (Figure 4.27). Groups from South America cluster to the left of the plot, while Caribbean groups are to the right. Central America and Garifuna are found centered. The St. Vincent Q haplotypes are clustered most closely to the Kali'na, a Cariban speaking group from French Guiana. The Honduran Coast more closely resembles haplotypes found in Costa Rica, in Central America, and the Kali'na and a group from Trinidad, an island of the coast of Venezuela.

Number of E1b1 haplotypes shared with Garifuna and Caribs in Central America, the Carribbean and Africa

Population	St. Vincent	Cristales	Rio Negro	Santa Fe	Bajamar	Corozal	Iriona	Central America	Afro-Caribbean	South America	Senegambia	Windward and Gold Coast	Bight of Benin	Bight of Biafra	West Central Africa	Southern Africa	Madagascar
St. Vincent*	4							40	139	21	35	25	73	**131**	58	78	15
Cristales		2	3	**9**	3	4	3	12	47	5	9	5	**52**	28	5	12	2
Rio Negro	2		**3**	**3**	2	1	2	13	91	13	19	11	61	**83**	35	61	12
Santa Fe	3			**7**	6	4	5	21	90	14	21	9	62	**70**	31	46	9
Bajamar	3				1			36	144	12	37	23	**92**	54	42	84	22
Corozal	2				**5**	1	3	12	38	7	1	9	37	**44**	10	17	2
Iriona	1				**4**		1	15	58	9	9	9	**62**	42	26	33	7

* Benn-Torres et al. 2015

Table 4.16. Number of Garifuna E1b1 haplotypes found in the literature.

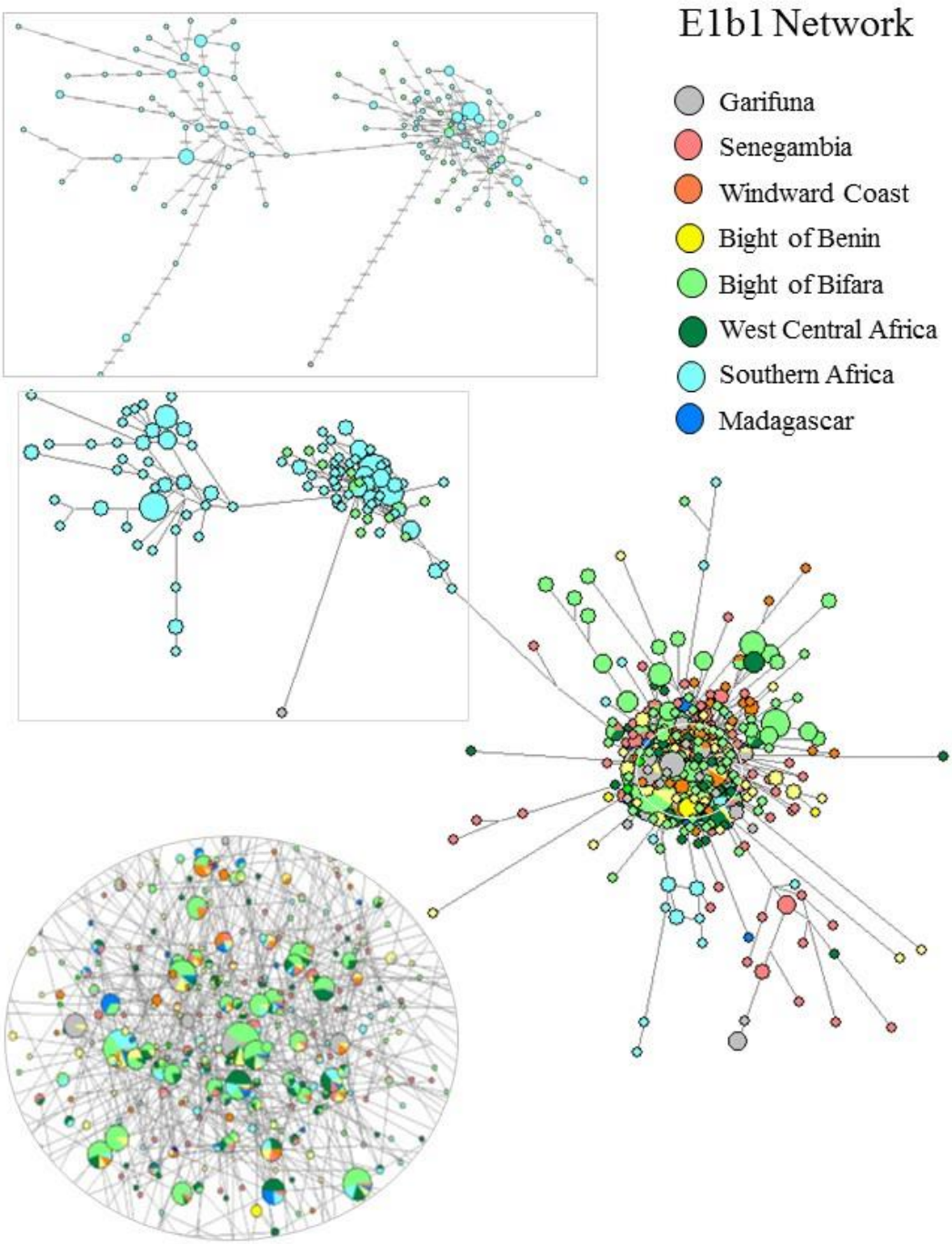

Figure 4.23. E1b1 median joining network with haplotypes from Garifuna and African populations.

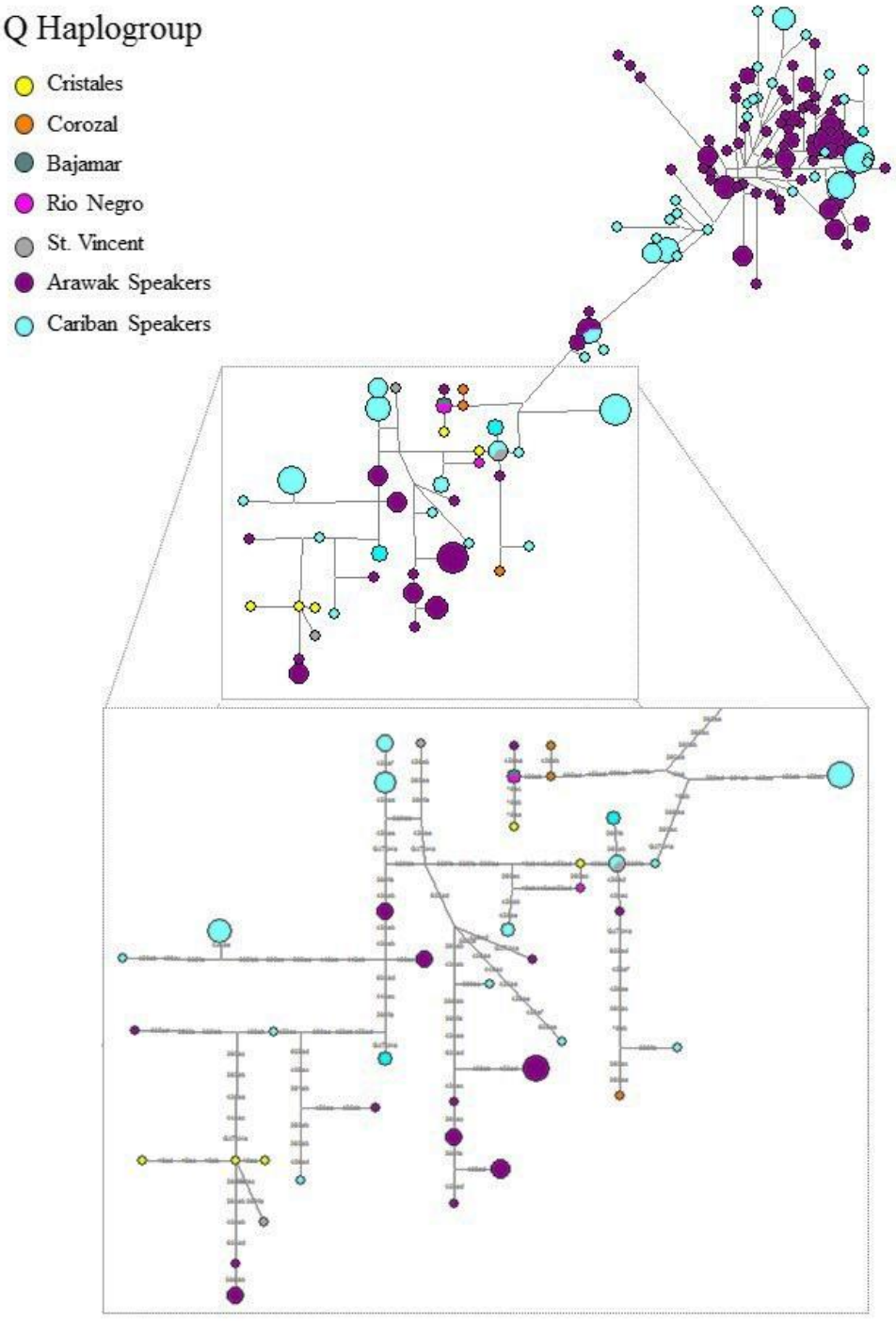

Figure 4.26. Median joining network of haplogroup Q haplotypes from Garifuna villages and Arawak and Cariban speakers from South America.

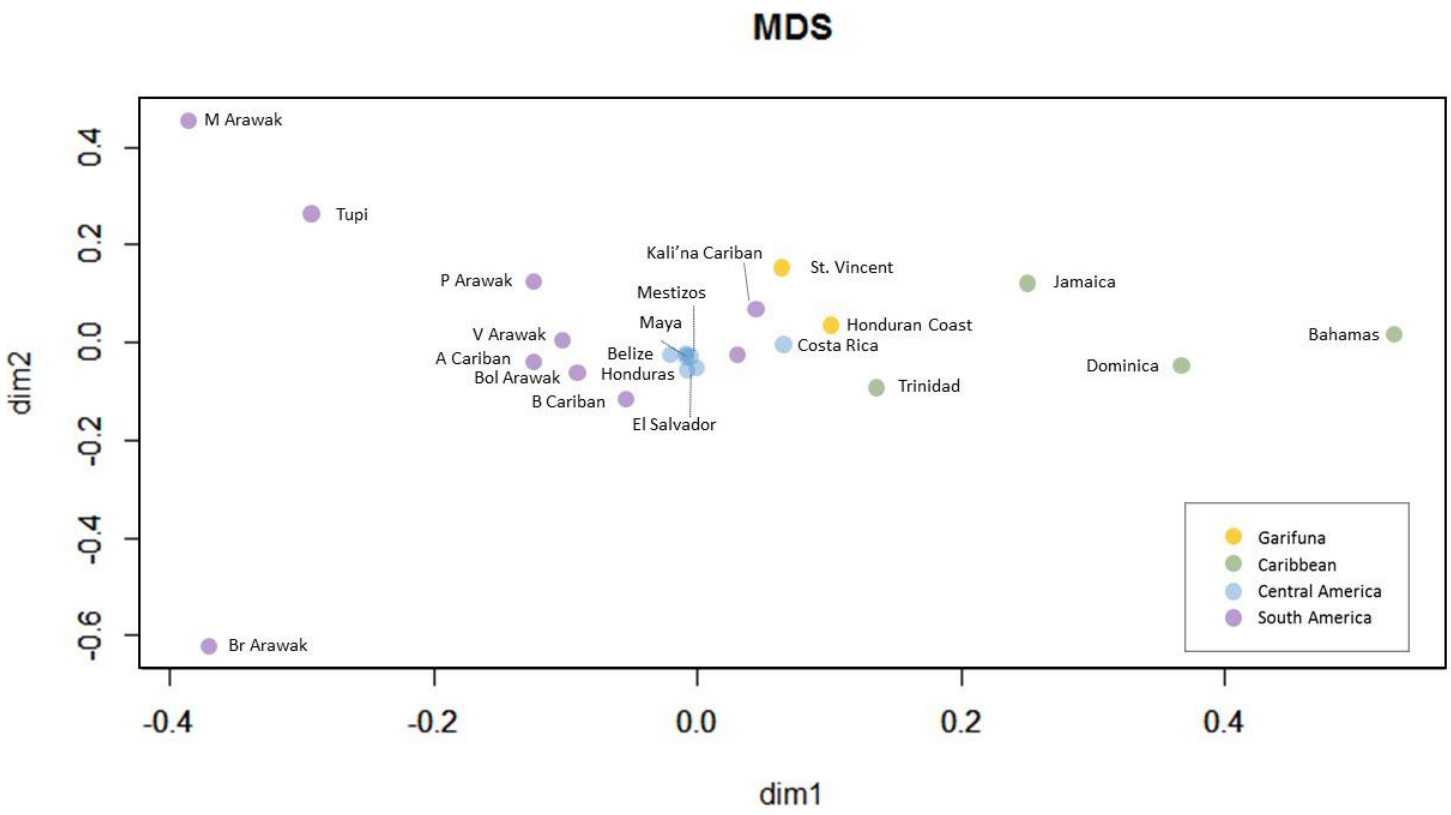

Figure 4.247. MDS plot of Slatkin's linearized FST distances between Q haplotypes found in Garifuna and other groups in the Caribbean, Central and South America.

Another network was constructed to visualize the relationship between the Q haplotypes found in Garifuna on the Honduran coast, and neighboring populations from Honduras (Figure 4.20). No haplotypes were shared between the Garifuna and coastal communities. However, most haplotypes (5 nodes) were only a single or two steps away from haplotypes found in other Honduran individuals. The most distant haplotype from other Honduran nodes was 5 mutational steps away, showing a close relationship between Q haplotypes belonging to the Garifuna and Q haplotypes found in other Honduran groups.

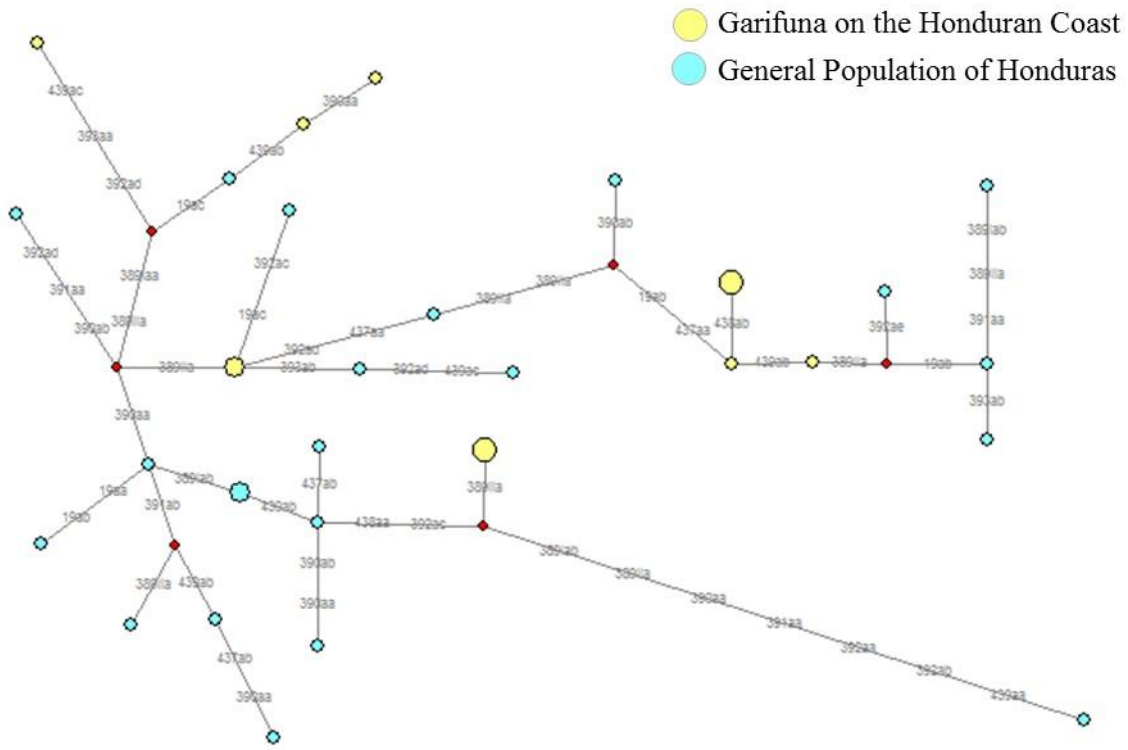

Figure 4.25. Median joining network of haplogroup Q haplotypes in Honduran Garifuna and in the general population of Honduras.

Pairwise F_{ST} scores between the Garifuna communities and all of the samples included in the study were graphed in Figure 4.29. The community of Cristales has the lowest F_{ST} scores outside when compared to Trinidad, St. Thomas, St. Vincent and Grenada in the Caribbean, and with West Central Africa and Madagascar. Rio Negro has the lowest F_{ST} scores when compared to Grenada and Trinidad, as well as West Central Africa. Santa Fe has the lowest F_{ST} scores when compared to African groups in West Central Africa, the Bight of Benin, and Senegambia. Corozal shows a smaller genetic distance to Madagascar and West Central Africa. Iriona has the lowest F_{ST} scores when compared to West Central Africa, the Bight of Benin and Senegambia, while Bajamar is lowest when compared to St. Kitts in the Caribbean, as well as Senegambia, West Central Africa, and the Bight of Benin. The Garifuna of St. Vincent has the smallest F_{ST} scores when compared to Afro-Caribbeans from St. Lucia and to African populations on Madagascar.

To further examine this relationship, an MDS plot of Slatkin's linearized F_{ST} values of Garifuna and comparative populations was made and shown in Figure 4.30. South American populations plotted in the right side of the plot, while Garifuna from Santa Fe, Iriona, Bajamar, and African populations plotted to the left. In the center, European, Caribbean, and Central American populations clustered with Rio Negro, Cristales, Corozal, St. Vincent, and Southern Africa and Madagascar. Cristales was found closest to Trinidad, while Rio Negro was most similar to English speaking African groups on St. Vincent. The Garifuna on St. Vincent and in Corozal were most closely plotted to St. Lucia and Jamaica in the Caribbean. Bajamar was closest to the African populations of West Central Africa and Senegambia. Iriona and Santa Fe did not cluster with the other populations.

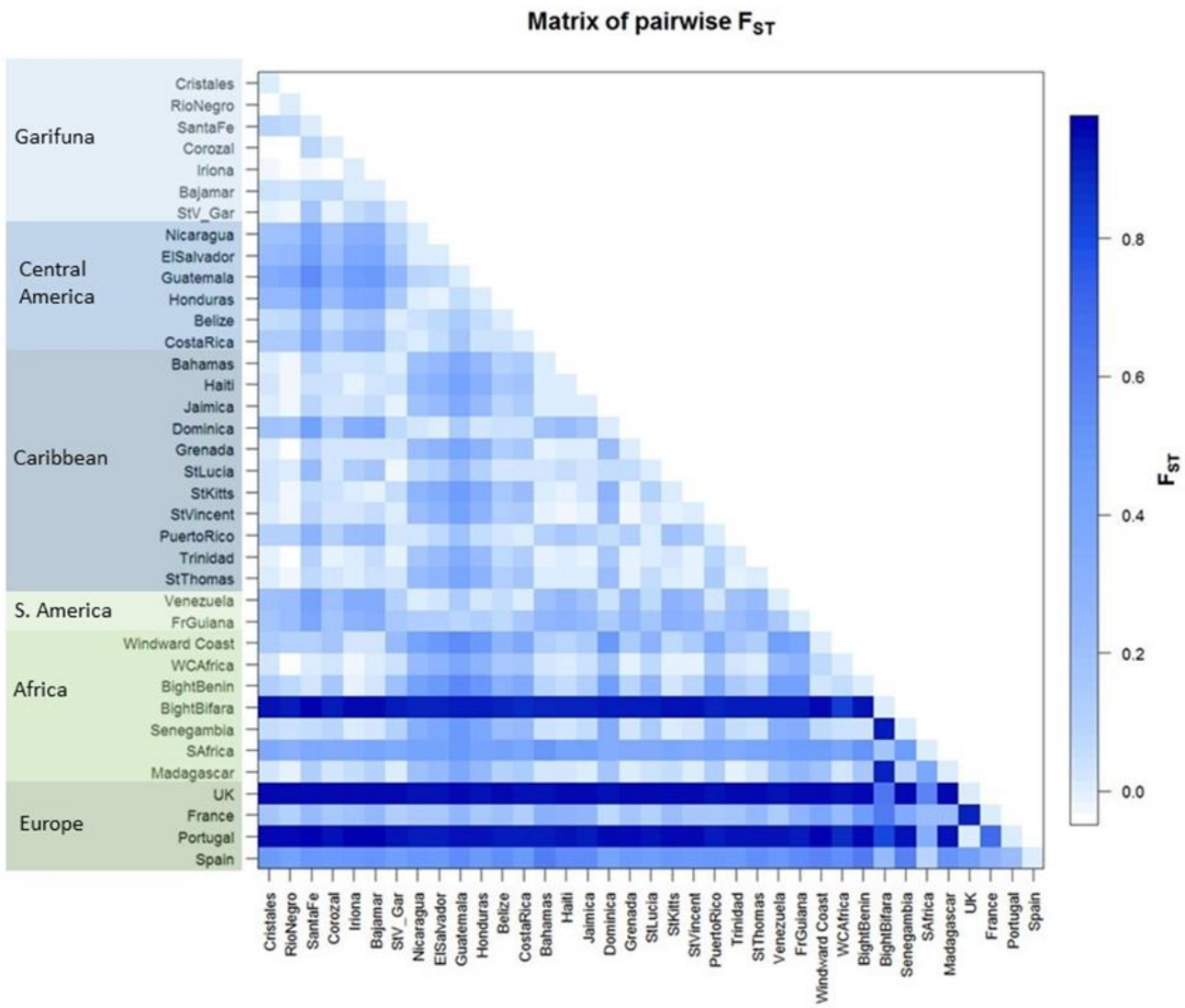

Figure 4.26. Matrix of pairwise FSTs in 7 Garifuna populations, and all comparative populations included in this study.

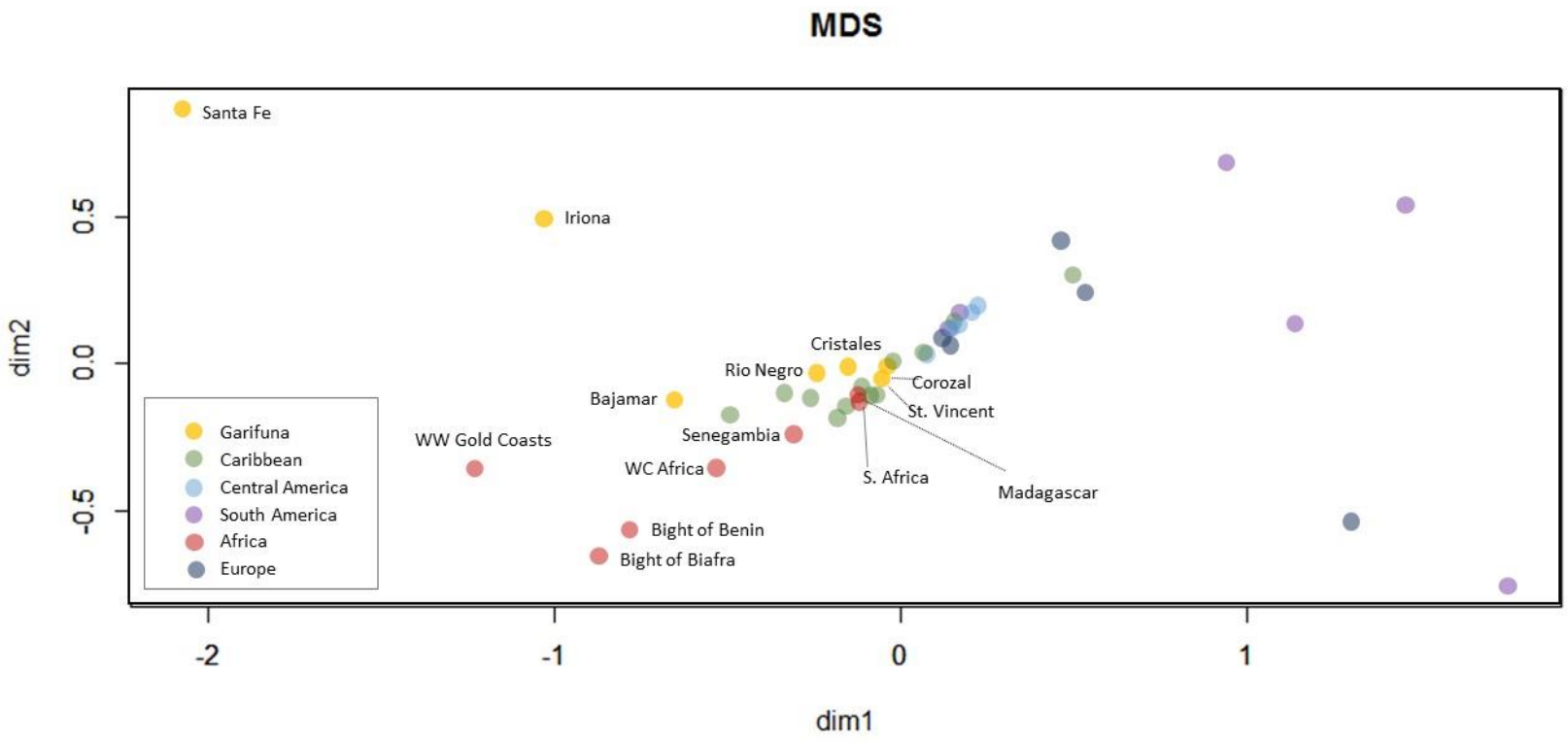

Figure 4.27. MDS plot of Slatkin's linearized FST distances between Garifuna Villages and comparative populations used in this study.

Intrapopulation measures between Garifuna as a single group, groups that may have contributed to the Garifuna gene pool, and other related populations, were graphed in Figure 4.31. The Garifuna display the lowest net pairwise differences between populations and the lowest average number of differences between populations when compared to the Native Caribbean and Afro-Caribbean populations pooled together, as well as to the African groups found in West Central Africa, Madagascar and Southern Africa. The Noir Marron, another African group found in South America, also had low values for these measures of population comparisons. Nei's distance between populations is lowest in Native Caribbean groups, Senegambia, West Central Africa and Madagascar, whereas the lowest pairwise difference between populations is seen between the Garifuna and Native Caribbean groups, and the Windward/Gold Coast.

Additionally, Slatkin's linearized F_{ST} scores between the Garifuna and other comparative populations was plotted using multidimensional scaling (Figure 4.32). Populations with large Native American contributions plot to the right of the plot. On the left of the plot are the African populations from Windward and Gold Coasts, West Central Africa, the Bight of Benin, and the Bight of Biafra. The Noir Marron, a group with a large African genetic contribution, plots near these African groups. Central and South American Admixed populations are found in the right center of the plot. The Garifuna are have the lowest F_{ST} values when compared to Madagascar and Southern African populations. Afro-Caribbean groups also cluster nearby, with Senegambia making up the forth closest group on the plot.

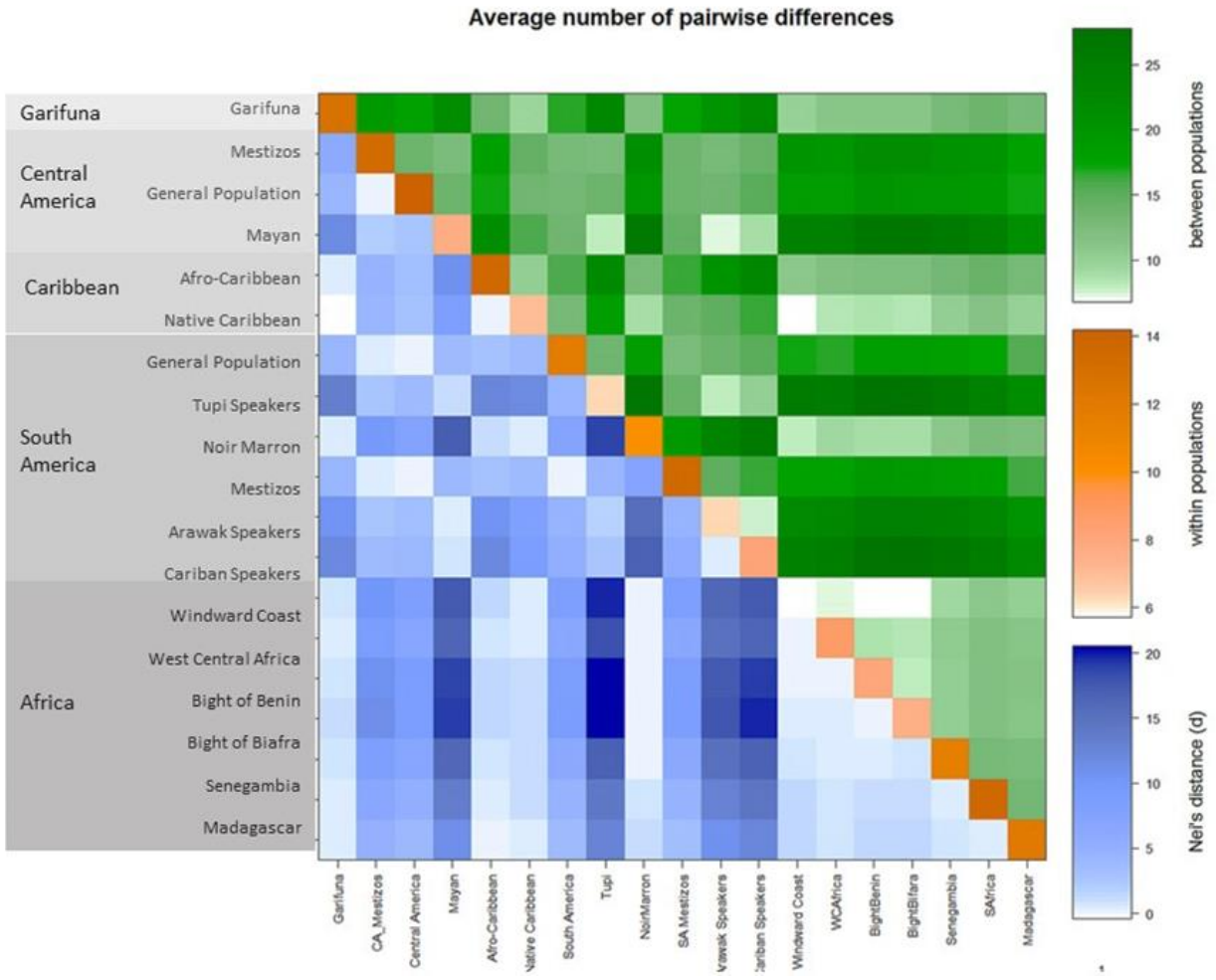

Figure 4.28. Average number of pairwise FSTs in Garifuna and other groups in Central and South America, the Caribbean, and Africa with the average number of pairwise differences within populations (orange), between populations (green), and net number of nucleotide differences between populations (blue).

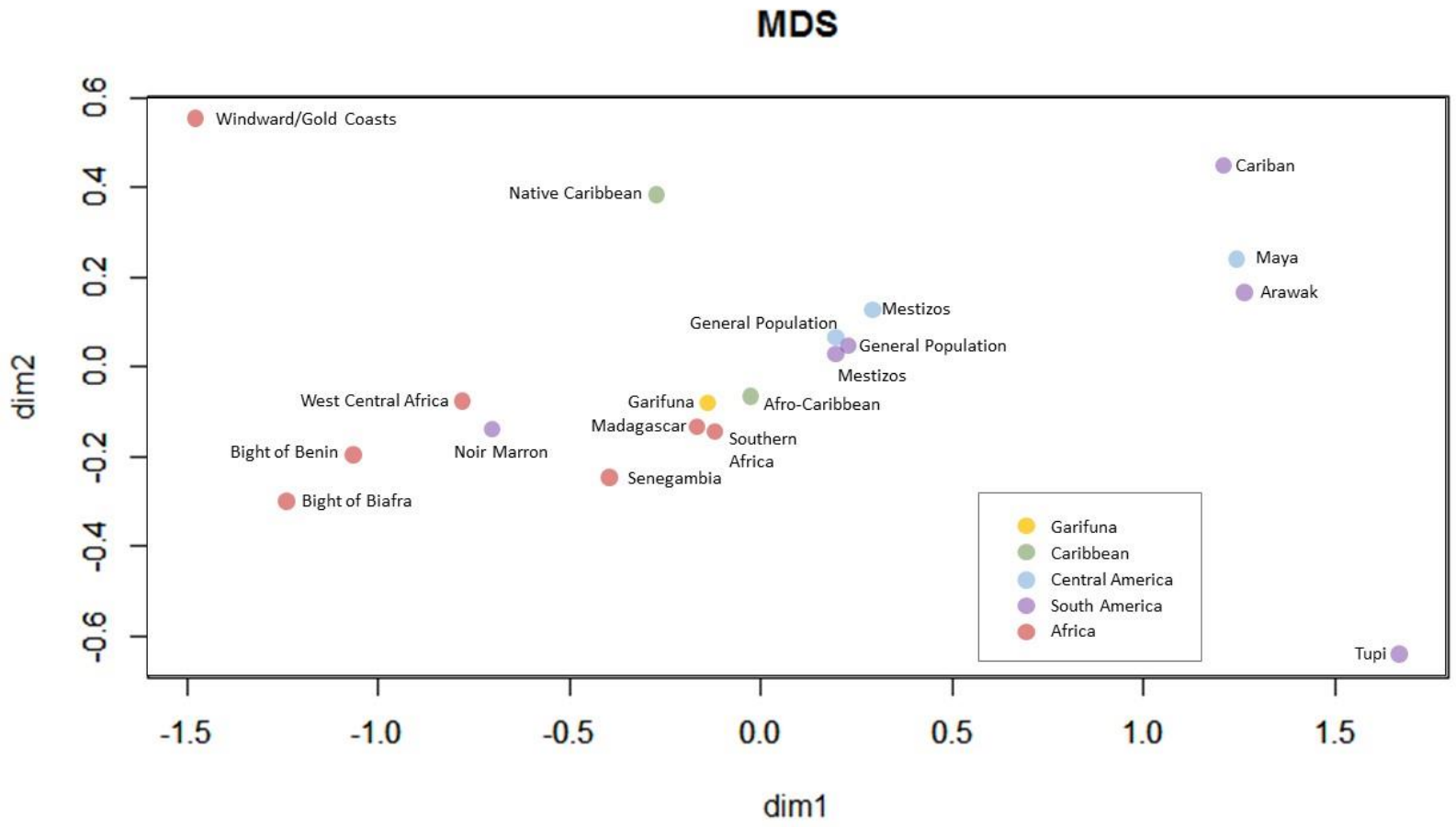

Figure 4.29. MDS plot of Slatkin's linearized FST distances between Garifuna and comparative populations included in this study.

Genetic distances versus geographic distances

A series of Mantel Test were also performed to examine the relationship between gene diversity and geography, and the relationship between mtDNA diversity versus Y-STR diversity (Table 4.17). No relationship was seen between Y-STR distances and geographic distances, nor between mtDNA distances and Y-STR distances. However, the test did indicate that there was a positive relationship between mitochondrial distances versus geographic distances (r=0.4629, p=0.0129).

Table 3.17. Mantel tests of mtDNA distances versus geographic distances, Y-STR distances versus geography distances, and mtDNA distances versus Y-STR distances.

Mantel Test	r	p
MtDNA vs. Geography	0.4629	0.0129
Y STRs vs. Geography	0.0473	0.4496
MtDNA vs. Y STRs*	-0.3661	0.7093

* Compared Cristales, Rio Negro, Santa Fe and St. Vincent

Chapter 5: Discussion

African Origins of the Garifuna

One of the origin stories of Africans in St. Vincent comes from different reports of shipwrecked slaves arriving in the 1630s. The origin of the ship varies in the telling, with some claiming it was under Spanish, Dutch or English control (Talyor, 2012). The origin of the slaves that were on the ship also varies, with some claims that they originated from Guinea (Senegambia region) and others claiming they were from the Bight of Benin, but reports do agree that survivors of shipwrecks were both men and women (Firschein, 1961; Talyor, 2012). Carib raids were also frequent in the 1500s to mid-1600s, and would have brought African slaves from nearby islands of the Greater and Lesser Antilles to Carib territories in Dominica and St. Vincent (Thomas, 1997). The prevailing current could also carry escaped slaves that had located a boat from islands, such as Barbados, directly to St. Vincent, however there were many slaves already on St. Vincent that could have escaped to Carib territories on the island (Talyor, 2012).

The majority of Africans that arrived in St. Vincent came between the years of 1517 to 1646 (Crawford M. H., Problems and Hypotheses: An Introduction, 1984; Thomas, 1997). The first shipments of African slaves to the Caribbean were sent to the Dominican Republic and Haiti in 1510, and by the 1520s, sugar production was beginning to use African slave labor. The request for slaves were directed towards slaves gathered just south of the river Senegal, out of the Senegambia region (Thomas, 1997). The Bight of Benin, an early provider of slave shipments stopped being a major slave port by 1553, and most of the Africans brought to the Caribbean were brought there before the 1550s. Other early slave shipments came out of ports that embarked from Ivory Coast and the Bight of Biafra. By 1689, the Royal African Company

of Britain had carried approximately 55,000 slaves to the Caribbean. Most of these were from the Windward and Gold Coasts and the Bight of Biafra, however, some were also brought from Senegambia, Angola, and to a lesser extent, the Bight of Benin (Thomas, 1997).

In contemporary populations of West Africa, where these early slaves were gathered, there is a high frequency of mtDNA haplogroups L2, L2a (though L2a is higher in Southeastern Africa), L1b, L3b and L3e, and a high frequency of Y chromosome haplogroup E1b1a (E-M2) (Thomas, 1997; Silva, et al., 2015; Arredi, et al., 2004). In Angola, there are high frequencies of mtDNA haplogroup L1c, L3e, and L0a, as well as a high frequency of Y haplogroup E1b1a (previously called E3a) (Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009; Silva, et al., 2015).

African Origins of the Maternal Markers in the Garifuna

The results of mtDNA analyses in this study indicate a divide between the islands in the Lesser Antilles, the Garifuna on Punta Gorda, and the coastal communities. The Garifuna of St. Vincent, and the Kalinago of Dominica have a lower African contribution to their mitochondrial gene pool, with African lineages present in 60 percent and 33 percent of the samples, respectively (Figure 4.4; Table 4.2). The lineages that are found in St. Vincent and Dominica are distinct from those found on the Central American coast, and are found on separate branches of the L0, L1 (Figure 4.11), and L3 networks (Figure 4.12; Table 4.2). The Kalinago do not share any African lineages with Garifuna in Punta Gorda nor the Central American coast. In Punta Gorda, the first Garifuna site after deportation from St. Vincent, 96 percent of the mtDNA lineages were of African origin (Figure 4.4; Table 4.2). Once on the coast, the mitochondrial haplotypes found were nearly all of African origin, except for one haplotype that was not

assigned to a mtDNA haplogroup, and a haplotype in Belize that belonged to Eurasian haplogroup W1g.

The Kalinago from Dominica were most closely related to African groups in Senegambia and the Bight of Benin, based on Nei's net number of nucleotides differences between populations and the Tamura and Nei's genetic distances (Figure 4.14; Figure 4.15) (Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009; Gonzalez, et al., 2006). Six individuals belonged to a subclade of L3, haplogroup L3e2, and another two individuals belong to subclade L3b/d. L3e is most frequent in northeastern Africa, but found in high frequencies (between 9-10 percent) in Senegambia, the Bight of Benin, as well as West Central Africa (Soares, et al., 2012). Three of the L3e2 haplotypes from Dominica in this study are also found in the Ivory Coast, suggesting an origin from the Windward or Gold Coasts (Brucato, et al., 2010). Haplogroup L1c1 is also present in 4 individuals in Dominica. L1c is commonly found among Bantu speaking populations and probably originated along the West Central African coast (Gonder, Mortensen, Reed, de Sousa, & Tishkoff, 2007). Haplogroup L1b, which is largely found in western Africa, was also found in the Dominica sample. Both haplogroups L1b and L1c are rarely found in Eastern and Southern Africa (Gonder, Mortensen, Reed, de Sousa, & Tishkoff, 2007). Three individuals belonged to subclades of L2: L2a, L2a1 and L2b. L2a is the most commonly found African haplogroup, and found in high frequencies in Ghana, Sudan and Mozambique, with subclade L2a1 found dispersed throughout the African continent (Silva, et al., 2015). None of the Kalinago haplotypes were shared with groups south of Gabon in Africa, suggesting a closer resemblance to African groups from Senegambia through the Bight of Benin, the earliest ports of the African slave trade.

The populations in St. Vincent, including the sample from Benn Torres et al. (2015), also displayed haplotypes characteristic of the earliest groups to be sent to the New World during the slave trade. Genetic distance measures (Nei's distance, average number of pairwise differences, and Tamura and Nei's distance) suggest a closest relationship to African groups from Senegambia and the Bight of Benin (Figure 4.14; Figure 4.15). In St. Vincent, most mtDNA lineages belonged to haplogroups L2a (4 individuals) and L2a1 (8 individuals), found throughout the African continent. These haplotypes were shared with comparative populations from Senegambia, Windward and Gold Coast, Bight of Benin, and West Central Africa (Gonzalez, et al., 2006; Brucato, et al., 2010; Fendt, et al., 2012; Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009). Two haplotypes belonged to haplogroup L3b, a haplogroup with the highest frequencies in Senegambia, (Soares, et al., 2012). One L3b haplotype was shared with individuals from Benin (Table 4.6) (Brucato, et al., 2010). Two haplotypes belonged to the L2 subclades L2b, most commonly found in West Africa, and L2e, found in West and West Central Africa (Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009). One haplotype belonged to haplogroup L1b1 found in Western Africa. Similar to Dominica, the African haplotypes found in St. Vincent are more commonly found in populations that were locations of the early slave ports, particularly those from Senegambia (Table 4.6).

Most African haplotypes in Punta Gorda belong to haplogroup L3e1, which is found at high frequencies in Mozambique and Angola, but is distributed throughout Western Africa (Salas A. , et al., 2004; Soares, et al., 2012). The presence of 2 haplotypes belong to L0 and L0a2 also suggest a relationship to West Central or Southern Africa. L0 is commonly found in Southern and Eastern Africa, but appears in lower frequencies in the Senegambia, the Bight of Benin, and the Bight of Biafra, and West Central Africa, usually as subclade L0a and in some

cases L0d, which may explain the origin of these haplogroups in Garifuna of Punta Gorda (Silva, et al., 2015). Indeed, the average net number of pairwise differences when compared to African regions showed that Punta Gorda was most similar to West Central Africa (Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009). However, the average number of pairwise differences and Tamura and Nei's genetic distances, between Punta Gorda and African regions was lowest when compared to Senegambia and Bight of Benin (Figure 4.14; Figure 4.15). This relationship is probably due to the presence of L1 (1 haplotype), L1b (6 haplotypes), and L1c0 (7 haplotypes), found predominantly in Western Africa (Gonder, Mortensen, Reed, de Sousa, & Tishkoff, 2007), and shared between Punta Gorda and Senegambia, and West Central Africa (Table 4.6) (Carvalho, et al., 2011; Gonzalez N. L., 1984; Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009; Trovoada, et al., 2003). Several haplotypes representing subclades of haplogroup L2a and L2c were also found in the Punta Gorda sample. Because of the diversity in African haplogroups found in Punta Gorda, the origin of mtDNA lineages in Punta Gorda can generally be described as West African, with some contributions from southern Africa.

Genetic distance measures between populations show that the coastal Garifuna communities are most similar to African groups in Senegambia, the Windward and Gold Coasts, and in the Bight of Benin, again pointing to origins from some of the early slave ports (Figure 4.14; Figure 4.15). As a whole, the most common macrohaplogroup found on the Honduran Coast was L2. Most of the L2 haplotypes belonged to haplogroup L2a1, found in high frequencies in Cristales and the Honduran Coast (32%, 18%), and L2a found in a high frequency in Santa Fe (30%) (Table 4.2). As stated above, L2a haplotypes are dispersed throughout the African continent. However, most of the L2a haplotypes found in this study have been reported in Senegambia, the Windward and Gold Coast, the Bight of Benin, and in lesser frequencies in

West Central Africa (Table 4.6) (Carvalho, et al., 2011; Gonzalez, et al., 2006; Brucato, et al., 2010; Fendt, et al., 2012; Trovoada, et al., 2003; Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009). L1and its subclades are also found at a relatively high frequency (21%) in the Garifuna communities along the Honduran coast (Table 4.2). The most frequent haplogroup represented is haplogroup L1b1, which is found at its highest frequencies in West Africa, and is rarely found in Eastern and Southern Africa (Silva, et al., 2015; Gonder, Mortensen, Reed, de Sousa, & Tishkoff, 2007). L1 haplotypes from Cristales, Rio Negro and Santa Fe have been reported in Senegambia and West Central Africa (Carvalho, et al., 2011; Gonzalez, et al., 2006; Trovoada, et al., 2003; Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009).

There is evidence of southern African contributions in the coastal Garifuna gene pool. Haplogroup L3 is found in the Cristales, Santa Fe and the Honduran Coast sample from Salas et al. (2005). The L3 haplotypes on the Honduran Coast have been reported in West Central Africa, but the other L3 haplotypes were not reported in the comparative literature (Trovoada, et al., 2003; Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009). Most of the L0 haplotypes found on the Honduran coast belong to haplogroup L0a2, with 17 L0a2 haplotypes in Rio Negro and 1 in the Honduran coast that was reported by Salas et al. (2005) (Table 4.2). L0a2 haplotypes are usually found in southeastern Africa, and several L0 haplotypes from Rio Negro are shared with populations in West Central and Southern African groupings, suggesting some African contributions from groups that arrived later in the Atlantic Slave Trade history (Table 4.6) (Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009; Trovoada, et al., 2003; Tishkoff, et al., 2009). Additional L0 haplotypes were found in Cristales and Santa Fe, but were not found within any of the comparative data.

As with the coastal populations in Honduras, the Garifuna of Belize represent a largely West African gene pool, with the lowest genetic differences between populations seen between it and the Windward and Gold Coasts and the Bight of Benin (Figure 4.14; Figure 4.15). Most of the haplogroups represented in Belize belong to L2a (19%) and L2a1 (19%), with haplotypes shared with populations from Senegambia, the Windward and Gold Coasts, the Bight of Benin and West Central Africa (Table 4.2) (Carvalho, et al., 2011; Gonzalez, et al., 2006; Brucato, et al., 2010; Fendt, et al., 2012; Trovoada, et al., 2003; Coelho, Sequeira, Luiselli, Beleza, & Rocha, 2009). Haplogroup L1b1 also represented 19 percent of the sample, with two related haplotypes (Figure 4.11). Evidence for input from of the second wave of African slaves entering the Caribbean comes from the presence of 2 haplotypes belonging to haplogroup L0a2 (n=8) and the presence of three L3 subclades: L3e1a, L3e1, and L3f1 (Table 4.2). Salas et al. (2004), noted that no L3f1 haplotypes had been found in the Americas, and that this supported the idea that few Khoisan speaking groups, or East African groups were part of the Atlantic slave trade. The presence of this haplogroup in Belize (11.1% in the sample) suggests that they did not completely escape slavery, and that some African groups from the later part of the slave trade did make their way into the Garifuna gene pool. However, the 2 haplotypes (n=6) found in Belize differ by only two mutations, and the frequency of the haplogroup is probably the product of genetic drift (Figure 4.12). These results suggest that the majority of Belizean mtDNA lineages are of West African ancestry, but a subset of African ancestry is from southern parts of the African continent.

African Origins of Paternal Markers in the Garifuna

Overall the Garifuna together (Honduran coast and St. Vincent) showed a lowest Nei's and Slatkin's linearized F_{ST} genetic distances when compared with West Central Africa, Senegambia, and Madagascar, though the values are low between Garifuna and all African populations (Figure 4.31; Figure 4.32). The average number of pairwise differences between populations is lowest between Garifuna and the Windward and Gold Coasts (Figure 4.31). Furthermore, results of Y-STR analyses of six villages along the Honduran coast show differences in the amount of male African gene flow between the islands of the Lesser Antilles, the Honduran coast and Belize (Figure 4.29; Figure 4.30) (Benn Torres, et al., 2015; Phillips-Krawczak, 2012). The islands of St. Vincent and Dominica have low frequencies of haplogroup E1b1 (35% and 6%), while the total African input on the Honduran coast was (77%). Additionally, Belize contains the lowest frequency of E1b1 haplotypes at 28 percent (Phillips-Krawczak, 2012). Tracing the origins of populations by Y haplogroups alone is difficult, as haplogroup E1b1 is the most prevalent Y haplogroup in Africa (Trombetta, Cruciani, Sellitto, & Scozzari, 2011). Its prevalence and diversity makes it difficult to trace its subclades to a particular origin, and the network of E1b1 haplotypes in Garifuna and African populations show that many haplotypes are shared by multiple regions and cluster together (Table 4.16; Figure 4.25). For this reason, the 8 loci haplotypes from Dominica, Belize, and St. Vincent by Phillips-Krawczak (2012) were excluded from further analyses.

While, the Dominican and St. Vincent samples from Phillips-Krawczak (2012) did not include enough Y-STR loci to add to the analyses that were done in this study, the samples were compared to populations from Nigeria and Equatorial Guinea representing the Bight of Benin and Biafra, and Mozambique and Angola representing Southern Africa. None of the haplotypes

from Dominica were found in the literature, but E1b1 haplotypes from St. Vincent were shared with Equatorial Guinea, Mozambique and Angola (Phillips-Krawczak, 2012). St. Vincent haplotypes, 48 percent belonging to haplogroup E1b1, from Benn-Torres et al. (2015) were included in this analyses and compared to populations throughout Africa. Three E1b1 haplotypes were shared with all African source regions including Madagascar (Tofanelli, et al., 2009). However, these three haplotypes were most commonly shared with the Bight of Biafra, the Bight of Benin and Senegambia (Table 4.16) (Montano, et al., 2011; Tishkof, et al., 2007; Carvalho, et al., 2011; Rosa, Ornelas, Jobling, Brehm, & Villems, 2007; Fortes-Lima, et al., 2015; Larmuseau, et al., 2015). Six other haplotypes were shared with the only the West African groups above or those in the Windward and Gold Coasts, and West Central Africa (Fortes-Lima, et al., 2015; Montano, et al., 2011; Melo, et al., 2011; Tishkof, et al., 2007). St. Vincent Garifuna has the lowest pairwise F_{ST} scores when compared to Madagascar, and are found to be closest to it and Southern Africa in a plot of Slatkin's linearized F_{ST} scores (Figure 4.29; Figure 4.30) (Tofanelli, et al., 2009). Two haplotypes were only found in Southern African populations (Alves, Gusmao, Barbosa, & Amorim, 2003; Tishkoff, et al., 2009). Benn-Torres et al. (2015) suggests that these haplotypes largely represent West African lineages, particularly from the Bight of Biafra. These analyses support this claim for some of the haplotypes present. However, there is evidence that some of the lineages may be from southern parts of Africa, where the slave trade began to expand after the earlier settlement of St. Vincent.

The 6 villages along the coast are made up of 74 percent haplogroup E1b1a, and 3 percent E1b. All villages have haplotypes that have been reported in all of the African groups. Cristales, Rio Negro and Corozal have E1b1 frequencies between 60-77%, with all but three haplotypes belonging to the subclade E1b1a (Table 4.11). The lowest pairwise F_{ST} is found

when Cristales, Rio Negro, and Corozal are compared to West Central Africa (Figure 4.29) (Melo, et al., 2011; Tishkof, et al., 2007; Montano, et al., 2011). However, the relationship of Slatkin's linearizes FST scores show that Cristales and Corozal are most closely related to Southern Africa and Madagascar (Figure 4.30). Rio Negro is close to these more southern groups and Senegambia, and the village of Bajamar appears closest to West Central Africa in the MDS plot. However, the largest number of haplotypes that are shared with each village are from the Bight of Benin (Table 4.10) (Fortes-Lima, et al., 2015; Larmuseau, et al., 2015). Bajamar and Iriona have E1b1a haplotypes in 84% and 86% of their male participants (Table 4.11), and their lowest F_{ST} values are found when compared to the most of western Africa including the Windward and Gold Coasts, the Bight of Benin, West Central Africa, and Senegambia (Figure 4.29). All of the haplotypes from Santa Fe were assigned to haplogroup_E1b1a, had the lowest F_{ST} when compared to West Central Africa and the Bight of Benin, and had haplotypes that were reported most often in the Bight of Biafra (Table 4.16). Overall, the haplotypes from these villages provide evidence of mixed ancestry, with the coastal villages more closely resembling Western Africa with some Southern African influences.

Shipwrecks, Raids or Escaped Slaves?

It is possible that shipwrecks brought Africans to the St. Vincent shores. However, the diversity of mtDNA haplogroups found in all Garifuna populations make it unlikely that a single ship was the main source of all African lineages, particularly if the ship arrived during the early 1600s when slaves were still generally gathered slaves from a single region. However, on the island of St. Vincent, most of the mtDNA diversity could have been found in one of the original slave ports. On the coast, most of the mtDNA haplotypes appear to be from regions where the earliest slave ports were located (Senegambia, the Bight of Benin, the Windward and Gold

Coasts, and West Central Africa), but there is evidence of African lineages that could be of a Southern African origin, lineages that would have arrived at different times and on different ships. This diversity might better be explained through Carib raids on European control islands, or escaped slaves that made their way to St. Vincent when it was a refuge for runaways.

The story is less clear when examining the African Y haplotypes. Many haplotypes belonging to the haplogroup E1b1 on the Honduran coast are related by one or two steps, and may have originated from a few founding males. In addition, haplotypes found in St. Vincent are found in all Garifuna communities along the coast except for Cristales. Furthermore, most of the haplotypes resemble lineages that are most commonly found in the Bight of Benin and the Bight of Biafra. However, the results of different genetic differentiation tests between Garifuna populations and other groups show that many of the groups more closely resemble African populations in Southern Africa and Madagascar. If this was their origin, than many of the Y chromosome haplotypes found on St. Vincent, and in the villages on the coast, represent later admixture with groups of African origin, either escaped slaves or descendants of slaves that remained on St. Vincent after slavery was abolished in 1834.

Native American Origins of Garifuna Maternal Markers

The first people to reach St. Vincent are thought to have arrived around 2000 years ago, from migrations out of the Orinoco River Basin of Venezuela, with later migrations from the same region bringing more people to the Caribbean islands by the time Europeans arrived in the early 1500s (Fitzpatrick, 2015). The first wave has been suggested to be Arawak speaking groups from South America. Oral histories of the remaining native peoples in the Lesser Antilles recount a second migration by peoples that were descendants of Kalinago, Cariban speakers that conquered the original Arawak inhabitants and took them as their wives (Taylor, 2012; Allaire,

1980). There are two islands that still have a considerable Native Caribbean gene pool, and these are the islands of Dominica, inhabited by the Kalinago on the Kalinago reserve, and the Garifuna that are found on the island of St. Vincent. The island of Dominica and has the highest frequencies of Amerind mtDNA (67%) (Haplogroups A2 and C1). In this study, coastal communities were compared to the groups in the Lesser Antilles to examine the relationship of the Native American lineages.

Previous research in the Americas identified 4 major mtDNA haplogroups are present, with haplogroups A2 and C1 found in the Garifuna and Kalinago of the Lesser Antilles (Benn-Torres et al., 2015; Salas et al., 2004; Phillips-Krawczak, 2012). Haplogroup A is found at its highest frequencies in Central America, accounting for roughly 63 percent of Central American lineages, has a frequency of over 50 percent in North America, but is found in only about 12% of populations in South America (Lalueza Fox, 1996; Melton, Briceno, Devor, Bernal, & Crawford, 2007). Haplogroup C is found at its highest frequency in South America, roughly 20%, with only 6 percent of North American lineages belonging to this haplogroup (Lalueza Fox, 1996). Work with Garifuna suggests that the A2 and C1 haplotypes that are found in the Lesser Antilles are more related to South American haplotypes than to those found in Central America (Benn Torres, et al., 2015; Phillips-Krawczak, 2012; Salas A. , et al., 2004).

Most of the Amerind haplotypes in the Lesser Antilles belong to haplogroup C1 (26% in the Garifuna and 67% in the Kalinago), while a smaller percentage of A2 makes up the Lesser Antilles gene pool (14 percent in Garifuna, 10 percent in Kalinago) (Benn Torres, et al., 2015; This study). The Kalinago of Dominica and the Garifuna of St. Vincent do not share any A2 or C1 haplotypes, however both islands have a lower average pairwise distance with Cariban speakers from Panama (Kolman, et al., 1995), but a lower Nei's distances between them and

Arawak speakers from Peru (Sandoval, et al., 2013) and Central American Mestizos (Nenuz, et al., 2010) (Figure 4.14). An MDS plot of Tamura and Nei's distances shows that outside of African groups, the Lesser Antilles populations are more similar to Arawak speakers and Maya from Southern Mexico (Figure 4.15) (Gonzalex-Martin, et al., 2015). The A2 haplotypes in the Lesser Antilles form a network of distantly related branches, with Kalinago and Garifuna on opposite sides of the network (Figure 4.10). In a network that includes all A2 haplotypes found in Garifuna, Arawak and Cariban speakers, and neighboring Central American groups, most of the lineages from the Garifuna and Caribs form their own branches, most of which seem more closely related to South American populations than to the haplotypes found in Central America (Figure 4.16).

However, the C1 network shows a closer relationship between Kalinago and Garifuna lineages, with Garifuna haplotypes related to a star-like node of St. Vincent haplotypes by a few mutational steps (Figure 4.10). C1 haplotypes from the Lesser Antilles are more closely related to each other that to groups in Central America (Figure 4.17). While this suggests a closer relationship to South American groups, the relationship is unclear in the network, where a single ancestral node is shared between Garifuna, Kalinago, and Cariban speakers. However, haplogroup C1 is rarely found in southern Central American groups, and its presence in the Lesser Antilles suggests it has been passed down from groups that originally travelled to the Caribbean islands from South America (Melton, Briceno, Devor, Bernal, & Crawford, 2007; Lalueza Fox, 1996). In addition, ancient DNA studies of Ciboneys, an Arawak speaking group that lived in Cuba, revealed a high prevalence of C haplotypes, that were closely related to South American HVS-I haplotypes (Lalueza-Fox, Gilbert, Martinez-Fuentes, Calafell, & Bertranpetit, 2003).

Punta Gorda, and the Central American Coastal Garifuna had few Amerind haplotypes, and the haplotypes that were present were not closely related to those found on St. Vincent or Dominica. Only one individual from Punta Gorda had an A2 haplotype, and it appears to be somewhat related to Central American haplotypes (Figure 4.16). In the Honduran Coast sample from Salas et al. (2004), Nei's DA was lower between it and Central American and Arawak speakers, whereas the average number of pairwise differences is lower between it and Central American and Cariban speaking groups (figure 4.14). The Honduran Coast had 4 A2 haplotypes and 3 haplotypes that belonged to haplogroup C1. The A2 network in Figure 4.16 shows one node that is a single step from a node of Cariban speakers, with a second node is 3 steps away from Central American populations. In addition, Belize had an A2 haplotype, and a HVS-II sequence from Cristales indicated the presence of C1, with the deletion of nucleotide position 290-291. Overall the origin of haplotypes in Garifuna on the coast give a mixed result indicating that the Native American maternal history of the Garifuna includes South and Central American origins.

Native American Origins of Garifuna Paternal Markers

Compared to maternal markers, there is a much larger Native American contribution to the coastal populations. Most native Y chromosomal haplotypes belong to haplogroup Q, which makes up 75 percent of Native American Y chromosomes (Battaglia, et al., 2013). Belize has the highest frequency of Amerind haplogroup Q than any other sample site, including the islands in the Lesser Antilles (Figure 4.19, Table 4.11). Y haplogroup Q is found in all communities except for Santa Fe and Iriona, but both sites have smaller samples sizes of 14 and 7 individuals. Previous reports on Garifuna and Kalinago in the Lesser Antilles show Amerind haplogroup Q

present in both groups at 21 and 41 percent (Phillips-Krawczak, 2012; Benn Torres, et al., 2015). A network including Q haplotypes from St. Vincent Garifuna (Benn Torres et al., 2015) and South American Cariban (Roewer, et al., 2013; Mazieres, et al., 2011)and Arawak speakers (Roewer, et al., 2013; Mazieres, et al., 2011) showed some relationship between St. Vincent and South American Q lineages (Figure 4.26). One Q haplotype from St. Vincent was shared with Cariban speakers, and another was closest to two nodes of Cariban speakers. When Q haplotypes were analyzed separately, the population from St. Vincent had the lowest Slatkin's linearized F_{ST} when compared with the Kali'na, a Cariban speaking group from French Guiana (Figure 4.27). This close relationship lends support to the idea that Cariban speaking males may have been present on the island of St. Vincent ad taken Arawak speaking wives.

In communities on the Honduran coast, 12 percent of the male participants carried Q haplotypes and, similar to the mtDNA haplotype on the coast, showed mixed results. Haplotypes from Criastels, Rio Negro Cristales, and Corozal shared haplotypes with Arawak speakers. However, all of these haplotypes were also found in Belize, Guatemala and El Salvador, and one haplotypes from Rio Negro was also found in Cariban speakers. Three of these haplotypes clustered with Arawak speakers in Figure 4.20, but were similarly related to one haplotype found in the general population of Honduras (Matamoros, Yurrebaso, Gusmao, & Garcia, 2009). The other haplotypes from Cristales, Rio Negro and Corozal appeared more closely related to Cariban speakers than to Arawak speakers. Figure 4.27 shows the Honduran Coastal population closest to groups in Costa Rica, though a more distant relationship is shown between it, St. Vincent, the Cariban speakers from French Guiana, and a group from Trinidad. Networks of Q haplotypes in Figures 4.26 and 4.28 show are that the coastal haplotypes are nearly split, with

roughly half of the haplotypes most closely resembling South American groups, and the other half more closely resembling Central American haplotypes.

European Origins of the Garifuna?

Other continental contributions to the Garifuna gene pool could have occurred through interactions during the slave trade, or during later admixture with neighboring groups. Only one European mtDNA haplotype was found in a Belizean Garifuna, characterized as belonging to haplogroup W1g. Haplogroup W found in low frequencies in Eurasia, Eastern and Northern Europe, as India. The haplogroup probably originated in the Near East and expanded after the Last Glacial Maximum (Olivieri, et al., 2013). During the 1600s-1900s, two waves of indentured servants were brought to the Americas to form part of the labor force. Some 300,000 English, Germans, Irish, Scots and French were brought as laborers. In addition, roughly 500,000 East Indians were moved to the Americas and the Caribbean as indentured servants to British colonists (Roopnarnine, 2003). In Punta Gorda, Belize, where this haplogroup was found, there were various groups with mixed European and European ancestry including Creole and Mestizo groups. There is also a small portion of the population (8% in the 1994 Census) that claim East Indian ancestry (Haug, 2002). Either of these groups could be a source for the maternal W1g haplogroup found in the Garifuna of Belize.

Y haplogroups R1b and T were also found on the Honduran Coast. Haplogroup R1b is the most common haplogroup in Europe and probably expanded out of the Iberian Peninsula after the Last Glacial Maximum (Capelli, et al., 2003). It is found throughout Europe, with high frequencies in European groups that were involved in bringing slaves into the Caribbean, including British (62-69%), Dutch (70%), French (52%), Portuguese (56-60%) (Capelli, et al.,

2003; Rosser, et al., 2000; Pericic, et al., 2005). The origin of the four Garifuna R1b haplotypes could have been the result of admixture from any of these sources. Five Garifuna individuals also carried 2 related haplotypes belonging to haplogroup T (formerly K2). One haplotype was shared by Corozal, Bajamar and Iriona. Haplogroup T makes up only 1 percent of all Y chromosome lineages worldwide, and is found in low frequencies in the Middle East, Northeastern Africa, and Europe (Karafet, et al., 2008). Because of the rarity of haplogroup T, and the relatedness of T haplotypes in the Garifuna, it is likely that this haplotype represents a single admixture event that has been brought to a higher frequency in the population due to genetic drift.

Population Expansion and the Garifuna Diaspora

In 1797, 664 Garifuna men and 1362 women arrived on the island of Roátan, off the coast of Honduras. By then end of 1797, 1465 Garifuna had moved to Trujillo, establishing the first barrios of Rio Negro and Cristales (Talyor, 2012). Two decades later, when Britain abolished the slave trade, Garifuna men found their labor in demand and seasonal migration to labor opportunities in woodcutting and banana plantations began (Talyor, 2012). By the mid-1800s estimates of Garifuna population size ranged from 20,000 to 50,000 people, occupying 400 miles of cost in Nicaragua, Honduras, Guatemala, Belize, and Roátan (Firschein, 1961). This population growth would have required a high fertility rate in the early settlers of the Central American coast, with some estimates at 10.9 children per woman (Crawford, personal communication). Rapid population growth, coupled with repeated founder effects occurring as new villages began to form leaves evidence in DNA. Genetic drift can act on a population by decreasing diversity from one generation to the next. In addition, the diversity between Garifuna

communities would increase as the fission of communities is often along familial lines, called kin-structured migration (Mielke & Fix, 2006).

All communities found outside of the Lesser Antilles had a reduced mtDNA gene diversity, and all but Punta Gorda have fewer mtDNA haplogroups represented in their sample (Table 4.3; Table 4.2). The Garifuna group furthest from Trujillo, in Belize, displays the lowest level of diversity (Table 4.3; Table 4.2). Within each community, haplogroup composition varies. For example, L3 is found in high frequencies in Punta Gorda (46%), while found in small frequencies in Rio Negro (9%) (Figure 4.4; Table 4.2). Most haplotypes within African macrohaplogroups L0-L3 form distinct community clusters in the median joining networks shown in Figures 4.11 and 4.12. Amerind haplogroup A2 displays a similar pattern, with distinct haplotypes found in different communities (Figure 4.10). However, haplogroup networks for Amerind haplogroup C1, and African haplogroup L2a1 do show some evidence of the population events that have occurred in the Garifuna. The C1 network displays a star-like cluster that is rooted in Kalinago haplotypes, but also shared by a few St. Vincent haplotypes (Figure 4.10). A star-like cluster of L2a1 haplotypes has a large node shared by St. Vincent, Cristales, Rio Negro, Santa Fe, Belize and the Honduran Coast sample from Salas et al. (2004), with nodes branching off for haplotypes found in St. Vincent, Belize, the Honduran coast, and Cristales (Figure 4.12). As a matrifocal group, you would expect maternally related individuals to stay together, as land rights are often passed on from mother and daughter. Thus, when a new village is formed, it likely moves groups of related females.

A mismatch distributions of all Garifuna coastal communities mtDNA sequences (Figure 4.56) shows some evidence of a recent demographic expansion ($r=0.05$; $p=0.18$). However, each community examined separately show the Honduran Coast sample (Salas et al., 2004), Cristales,

and Belize exhibit multimodal distributions with high raggedness values signaling that these communities have not undergone a recent demographic expansion (Figure 4.7). In other words, despite the expansion and rapid population growth seen in the Garifuna as a whole, individual communities display signals of drift. This is supported by a mantel test that showed a relationship between mtDNA genetic diversity and geographic distance ($r = 0.4629$; $p = 0.0129$).

While uniparental markers such as mtDNA and the Y chromosome have an effective population size one forth of nuclear markers, the Y chromosome is particularly subject to the effects of genetic drift (Rosser, et al., 2000). When a dominating group of males makes a significant contribution to a gene pool, the amount of Y chromosome diversity can be reduced. This effect, called the Genghis Kahn effect, can be seen by the effects of Genghis Kahn's regin, where a particular Y chromosome lineage is now carried by 8 percent of all males in Asia (Jobling, Hurles, & Tyler-Smith, 2004). The earliest Garifuna groups on the island of St. Vincent were patriarcical, and males of high status often took multiple wives. It could also explain why several Y haplotypes on the Honduran coast appear to have originated on the island of St. Vincent, or at least have a stronger relationship with South American lineages. If these haplotypes represent individuals that descended from men with higher status, they would have been added at a higher frequency to the population and more likely to persist in the Garifuna gene pool. While, the Garifuna today are a matrifocal society, men are encouraged to have multiple partners, while women are expected to have one partner at a time (Gonzalez N. L., 1984). Evidence of drift in the Garifuna Y chromosome included lower diversity measures in the 6 coastal communities when compared to St. Vincent (Table 4.13). This can be observed in the Networks of 27 loci haplotypes found in Rio Negro, Cristales, and Santa Fe, where haplotypes are separated by long tracks of mutations, with only a few haplotypes separated by one or two

steps (Figure 4.21). When the network is reduced to 10 loci, to include the villages of Bajamar, Iriona, and Corozal, there does appear to be some star-like clusters in the E1b1 network of all Garifuna sample from the coast. This group of related nodes includes haplotypes from all Garifuna villages and may represent an expansion event of African lineages (Figure 4.22).

These results support the history of Garifuna along the coast, a history that has undergone a series of bottlenecks reducing the diversity in Garifuna villages. Despite the actions of drift, the coastal Garifuna still display a relatively high amount of diversity for a group that began as 2,000 individuals. This high level of diversity might be explained by other forces acting on the population.

Evidence of Admixture

Within the first 50 years of Garifuna settlement of the coast, the Garifuna population had grown from an initial 2000 individuals to between 20,000 and 50,000 people (Firschein, 1961). Garifuna have traditionally had a high birth rate, but a high birth rate alone was not the only cause for an increase in population size. Garifuna at every current location lived alongside other groups, some of African descent, some of Native American ancestry, and many admixed populations. This admixture is a part of the Garifuna story, and explains some of demographic growth and success of the population.

Today, around 2,000 Garifuna live in the Bay Islands, with most of the residents living in the village of Punta Gorda, on Roátan (Richards, 2003). The mtDNA gene diversity and the average number of pairwise difference is higher in Punta Gorda than the three Garifuna villages on the coast; the average number of pairwise differences is higher than that found in any Garifuna or Kalinago sample, indicating that there are many haplotypes found in the population

that different geographical origins (Table 4.3;Table 4.2). This would be partially expected as it was the first home of Garifuna after their deportation from St. Vincent. However, most of the original Garifuna on the island left, leaving approximately 200 Garifuna behind, and it is unlikely that this small original group contained this much diversity (Talyor, 2012). The majority of African descent people living on Punta Gorda are the Inglés, or Creoles, an English speaking people that are the descendants of British slaves, and reports of admixture with this group were noted in this study. Evidence of admixture in Punta Gorda can be seen in the high frequencies of haplotypes belonging to haplogroup L3 and its subclades. Several of the Punta Gorda haplotypes form distinct branches of the L3 network, a branch not shared by groups in the Lesser Antilles (Figure 4.12).

The earliest villages of Rio Negro and Cristales were established in Trujillo, once the capital of Honduras (Herrera-Paz E. F., 2017). At the time of Garifuna arrival, several other groups were in the area. An African slave depot was in Trujillo as early as 1530, providing labor to mines that were being established in the area (Thomas, 1997). Miskito groups were also in the region at the time of arrival. Other African groups included French speaking Africans and Creoles that worked on banana plantations (Salazar-Flores, et al., 2015). This location would have brought Garifuna in contact with various groups in Honduras, and opened the way for admixture that introduced L3d haplotypes to Rio Negro and Cristales, haplotypes that are not found in the rest of the coastal population or in the Garifuna on Roátan or St. Vincent. In addition, L0 haplotypes in Cristales and Rio Negro appear distinct from other L0 haplotypes and may have been brought into the Garifuna gene pool from these groups. They could also, however, represent lineages that were lost on St. Vincent when Garifuna of African phenotypes were removed from the island.

Increased migration in response to environmental and social stressors

An estimated 14,500 Garifuna live in the Department of Colon (Richards, 2003). Garifuna villages along the coast of Honduras consist of 1,500-4,000 individuals (Herrera-Paz E. F., 2017). In a small population size, genetic drift has a stronger influence on the genetic makeup of the community, and the effects of population divisions and increased migratory movements as adults seek job opportunities farther away, can leave marks on the genetic makeup of a population. More recent history has played a role in shaping the composition of Garifuna villages. For example, over the last 50 years, roads were built along the coast, and job opportunities in industrial areas in the west have been increasing the movement of people away from the coastal villages (Herrera-Paz E. F., 2017). In addition, the last 20 years have seen several flooding events that have displaced Garifuna from 8 villages, including Iriona, along the coast (Wrathall, 2012). These events included Hurricane Mitch (1998), which displaced over 200 households in the Garifuna village of Santa Rosa de Aguan, and Tropical Depression Gamma (2005) that destroyed fishing industry and beef production in some coastal communities (Wrathall, 2012).

In addition, the high diversity in Punta Gorda may be due to an increase in migration to Roátan. The island has become a major tourist attraction over the last few decades, with the Honduran government encouraging foreign investors to build hotels there. Punta Gorda has its own airport, so travelers can fly directly to the island from most major U.S. cities. As a result, many Garifuna have found work in the businesses that have been established there. Nearly a third of the men and women that participated in this study resided in, but were not born in, Punta Gorda, and the increased diversity may be due to individuals moving to the island for work

(Figure 4.3). This more recent migration may be increasing the diversity in the Garifuna gene pool on the island.

Migration has long been a cultural practice in Garifuna society, and used as a means to supplement a subsistence economy that was largely based on fishing and agriculture. Even work sought in the United States and larger cities in Central America were meant to supplement an already adequate subsistence. However, this has changed within the last 20 years. In 1992, a Law for the Modernization and Development of the Agricultural Sector was passed in Honduras, which resulted in the loss of Garifuna lands once used for agriculture, or homes that effectively moved them away from their main form of subsistence. As a result migration labor is no longer necessary for supplementing Garifuna subsistence, but increasingly necessary for supporting it (Brondo, 2007). This new forced migration is aging the Garifuna population villages. It is now common for both women and men to leave the home in search of work, often leaving children in the care of grandparents, aunts or siblings.

Evidence of historical and recent immigration can be seen in the sharing of Y chromosome haplotypes between villages. Several E1b1and Q haplotypes are shared between several Garifuna villages (Figure 4.21; Figure 4.22). In addition, the presence of two related haplotypes belonging the rare haplogroup T in the villages of Iriona, Corozal and Bajamar shows evidence of male migration between villages. A mantel tests found that, unlike mtDNA distances compared to geographic distance, the Y distances did not show a relationship with geography (Table 4.17). The recent increase in migration by both sexes is likely to further influence the genetic structure seen in Garifuna villages.

Chapter 6: Conclusion

The Garifuna of Punta Gorda and the Honduran Coast exhibit traces of the original admixture between African, Amerindian, and European peoples on the island of St. Vincent. However, since 1797, when individuals with African phenotypes were forcibly moved to Punta Gorda, the Garifuna have spread to throughout Central America. Villages along the coast, settled by a series of founder effects, followed by the loss of individuals looking for work in more developed areas, and admixture with neighboring groups, have each acquired distinct genetic signatures. This is particularly evident in the villages Rio Negro and Cristales, both located within Trujillo, that have very different frequencies of mtDNA and Y chromosomal haplogroups.

The origins of Garifuna are largely found in West Africa, with Amerind and European contributions. The African origin of mtDNA markers found in the Garifuna of St. Vincent are generally where the early ports of the Atlantic Slave trade set out for the Caribbean in the 1500-1600s. However, there is evidence that later southern African arrivals also contributed to the African gene pool, somewhat on the island of St. Vincent, but particularly in the coastal communities, where admixture with Creole, Mestizo, and other admixed groups have been documented. While some African Y markers appear related to populations that participated in the early waves of the slave trade, most Y haplotypes found in the Garifuna show a general African origin, and appear more closely related to Southeastern populations. These results support admixture with other African groups that were brought to the Caribbean.

Native origins of the Garifuna are found in high frequencies of Native American mtDNA and Y haplogroups found in on St. Vincent. The mtDNA haplotypes belonging to haplogroups

A2 and C1 on St. Vincent are most similar to others found in the Lesser Antilles, and are more related to South American lineages than they are to those found on the Central American coast. The Y haplogroup Q haplotypes found in St. Vincent show a similar result, and are most related to haplotypes seen in Kali'na speakers, a Cariban speaking group found in French Guiana.

MtDNA and Y chromosome haplotypes found in Punta Gorda and the Honduran Coast show evidence of admixture. The few maternal haplotypes of Native American origin resembled groups from both South and Central America. The frequency of Native American markers in the Y-chromosomes in this study were higher than what was found in mtDNA. Similar to mtDNA results, these haplotypes indicate that roughly half of the Q haplotypes were from the Lesser Antilles, while the other half were likely due to admixture with neighboring groups such as the Miskito or Mestizos found on the coast.

In addition to African and Native American contributions to the Garifuna gene pool, evidence of European gene flow can be seen with the presence of Y haplogroups R1b and T that are found along the Honduran coast. It is unclear whether these haplotypes were the result of admixture with Europeans on St. Vincent or the result of admixture with coastal populations. In addition, a single Eurasian haplogroup, W1g, was found in a Garifuna community in Belize. This haplogroup was likely brought into the Garifuna community through admixture with neighboring groups of East Indian ancestry, though European admixture cannot be ruled out.

The Garifuna of Central America have undergone a series of bottlenecks, from their removal from the island of St. Vincent, to the splintering off of groups to form different villages along the coast. These bottlenecks can be detected in the lower levels of diversity seen from Trujillo to the groups in Belize, particularly in the mtDNA diversity in the coastal communities. As the Garifuna population has expanded from the original 2000 coastal settlers, to the roughly

300,000 Garifuna, the Garifuna have formed new villages along the Central American coast. These villages now number over 60, stretching from Belize to Nicaragua. The differences in mitochondrial haplogroup composition in each community is the result of matrilocal residence patterns, with new villages formed by groups of related Garifuna women. Gene flow, between villages, as men move for work can be seen in the sharing of several Y lineages throughout the sample. In addition, gene flow from outside groups has contributed to the Garifuna gene pool.

Migration has always been a part of Garifuna culture, as they were a group born out of migration. Current forces have increased migration in Garifuna communities. The high level of diversity in Punta Gorda is evidence of this shift, as people migrate for labor opportunities in tourism. Meanwhile, coastal communities impacted by environmental disasters are losing genetic diversity as the social networks that were once established have dissolved. In other coastal communities, loss of land to agriculture and tourism has increased the dependence of wages made outside of the home communities. These forces will continue to shape the genetic structure of the Garifuna of the Honduran Coast.

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Appendix A: Sources for Populations Used for Comparison in this Study.

Table A.1. Sources of mtDNA HVS-I and HVS-II sequences used in this study.

Region	Group	Country/Island	Location	n	Source
Central America	Garifuna	Honduras	Cristales	31	**Current Study**
	Garifuna	Honduras	Rio Negro	37	**Current Study**
	Garifuna	Honduras	Santa Fe	46	**Current Study**
	Garifuna	Honduras	Honduran Coast	44	Salas et al. 2005
	Garifuna	Belize	Punta Gorda, Barranco	54	**Phillips-Krawzack 2012**
	Mestizos	Nicaragua	Nicaragua	162	Nunez et al . 2010
	Ngobe	Panama	Cariban Speakers	46	Kolman et al. 1995
	Maya	Mexico	Southern Mexico	312	Gonzales-Martin et al. 2015
Caribbean Islands	Garifuna	Roatan	Punta Gorda	56	**Current Study**
	Garifuna	St. Vincent	Fancy, Owia, Sandy Bay, Greiggs	31	**Phillips-Krawzack 2012**
	Garifuna	St. Vincent	Kingstown, and north	65	Benn-Torres et al. 2015
	Kalinago	Dominica	Kalinago Reserve	53	**Phillips-Krawzack 2012**
	First Peoples		Trinidad	23	Benn-Torres et al. 2015
South America	Machiguenga and Yanesha	Peru	Amazon, Arawak speakers	29	Sandoval et al. 2013
	Noir Marron	French Guiana	Saint Laurent du Maroni, Maripasoula, Papaichton	142	Brucato et al. 2010
	African American	Columbia	Choco	49	Salas et al. 2005
Senegambia			Guinea Bissau	79	Carvalho et al. 2011
			Mali	124	Gonzales et al. 2006
			Mauritania	64	Gonzales et al. 2006
Windward/Gold Coast			Ivory Coast	190	Brucato et al. 2010
			Ghana	191	Fendt et al. 2012
Bight of Benin			Benin	150	Brucato et al. 2010
Bight of Biafra			Camroon	30	Tishkoff et al. 2009
West Central Africa			Sao Tome	103	Trovoada et al. 2003
			Angola	365	Coelho et al. 2009
Southern Africa			Sout Africa	19	Tishkoff et al. 2007
			Tanzania	278	Tishkoff et al. 2007

Table A.2. Y-STR data used in this study.

Region	Group	Village/Country/Island	n	Source
Central America	Garifuna	Cristales, Honduras	15	This study
	Garifuna	Rio Negro, Honduras	13	This study
	Garifuna	Santa Fe, Honduras	14	This study
	Garifuna	Corozal, Honduras	20	Matamoros (unpublished)
	Garifuna	Iriona, Honduras	7	Matamoros (unpublished)
	Garifuna	Bajamar, Honduras	26	Matamoros (unpublished)
	General Population	Honduras	128	Matamoros et al. 2009
	Mestizos	Nicaragua	165	Nunez et al. 2010
	Maya	Guatemala	99	Cardosa et al. 2016
	Mestizos	Guatemala	115	Martinez-Gonzalez et al. 2012
	General Populaiton	El Salvador	150	Monterrosa et al. 2010
	General Population	Belize	157	Flores et al. 2005
	General Population	Costa Rica	100	Villalta et al. 2008
Caribbean	Garifuna	Kingstonw, St. Vincent	25	Benn-Torres et al. 2015
	First Peoples	Trinidad	5	Benn-Torres et al. 2015
	Afro-Caribbean	Dominica	21	Benn-Torres et al. 2007
	Afro-Caribbean	Grenada	35	Benn-Torres et al. 2007
	Afro-Caribbean	St. Lucia	24	Benn-Torres et al. 2007
	Afro-Caribbean	St. Kitts	33	Benn-Torres et al. 2007
	Afro-Caribbean	St. Vincent	21	Benn-Torres et al. 2007
	Afro-Caribbean	Trinidad	32	Benn-Torres et al. 2007
	Afro-Caribbean	St. Thomas	134	Benn-Torres et al. 2007
	Afro-Caribbean	Jamaica	53	Benn-Torres et al. 2007
	Afro-Caribbean	Puerto Rico	121	
	Abaco, Eleuthera, Exuma, Grand Bahama, Long Island, New Providence	Bahamas	426	Simms et al. 2013
	General Population	Haiti	123	Simms et al. 2013
	General Population	Jamaica	141	Simms et al. 2013
South America	Arawak sp	Bolivia	52	
	Arawak sp	Venezuela	19	
	Arawak sp	Brazil	32	
	Cariban Sp	Brazil	55	
	Mestizos and Choco	Columbia	93	Romero et al. 2008
	Caracasn, Maracaibo	Venezuela	173	Borjas et al. 2008
	Apalai, Emerillon, Kali'na, Matsiguenga, Palikur, Wyampi	French Guiana	129	Mazieres et al. 2010
	Noir Marron	French Guiana	42	Brucato et al. 2010
Senegambia	Balanta, Bijagos, Felupe-Djola, Fulbe, Mandenka, Nalu, Papel	Guinea Bissau	227	Rosa et al. 2007
	General Populaiton	Guinea Bissau	33	Carvalho et al. 2011
	Ahziz and Yacouba	Ivory Coast	60	Fortes-Lima et al. 2015
Windward and Gold Coasts	Bariba, Yoruba, Fon, Berba, Dendi	Benin	196	Fortes-Lima et al. 2015
Bight of Benin	Bariba, Berba, Dendi, Fon	Benin	120	Larmuseau et al. 2015
Biaght of Biafra	Yoruba	Nigeria	12	Tishkoff et al. 2007
West Central Africa	Noth Bateke	Angola	19	Montano et al. 2011
	Bakongo, Kimbundo, Obimbundo	Angola	166	Melo et al. 2011
Southern Africa	Ovambo	Namibia	54	Fujihara et al. 2009
	Datog, Burunge, Mbugwe, Turu, Hadza, Sandawe, Sukuma	Tanzania	239	Tishkoff et al. 2007
	Maputo	Mozambique	122	Alves et al. 2003
Madagascar	Antaisaka, Antandroy, Antanosy, Merina	Madagascar	110	Tofanelli et al. 2009
Europe	Dutch	Netherlands	2085	Westen et al. 2015
	General Populaiton	United Kingdom	300	King et al. 2006
	Ireland	United Kingdom	855	McEvoy and Bradley 2006
	England	United Kingdom	94	Busby et al. 2011
	Scotland	United Kingdom	20	Busby et al. 2011
	Corsica	France	62	Ghiani et al. 2009
	General Population	France	14	Busby et al. 2011
	General Population	Portugal	23	Busby et al. 2011
	General Population	Spain	148	Marten et al. 203
	General Population	Spain	245	Busby et al. 2011

Table A.3. Populations included in haplogroup Q network. Haplotypes were based on Y-STR loci DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439, DYS448, DYS456, DYS458, DYS635, and Y-GATA H4.

Group	Country	Population	n	Source
Garifuna	Honduras	Cristales	5	Current Study
		Rio Negro	2	Current Study
		Corozal	3	Current Study
		Bajamar	1	Current Study
	St. Vincent	Kingstown	3	Benn-Torres et al. 2015
Arawak Speakers	Bolivia	Ignaciano	6	Roewer et al. 2013
		Trinitario	36	Roewer et al. 2013
		Mojeno	10	Roewer et al. 2013
	Venezuela	Wayampi	19	Roewer et al. 2013
	Brazil	Terena	32	Roewer et al. 2013
	French Guiana	Matsiguenga	12	Mazieres et al. 2010
		Palikur	25	Mazieres et al. 2010
Cariban Speakers	Brazil	Tiriyo	35	Roewer et al. 2013
		Arara	20	Roewer et al. 2013
	French Guiana	Apalai	25	Mazieres et al. 2010
		Kali'na	15	Mazieres et al. 2010

Table A.4. Populations included in haplogroup E1b1 network. Haplotypes were based on Y-STR loci DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS437, DYS438, DYS439, DYS448, DYS456, DYS458, DYS635, and Y-GATA H4.

Region	Country/Village	n	Source
Garifuna	Cristales	9	Current Study
	Rio Negro	10	Current Study
	Santa Fe	27	Current Study
	Corozal	13	Current Study
	Bajamar	21	Current Study
	Iriona	7	Current Study
	St. Vincent	13	Benn-Torres et al. 2015
Senegambia	Guinea Bissau	151	Rosa et al. 2007; Carvalho et al. 2011
Windward/Gold Coast	Ivory Coast	74	Fortes-Lima et al. 2015
Bight of Benin	Benin	146	Fortes-Lima et al. 2015; Larmuseau et al. 2015
Bight of Biafra	Camroon	155	Montano et al. 2011
	Gabon	304	Montano et al. 2012
	Nigeria	129	Montano et al. 2013; Tishkoff et al. 2007
West Central Africa	Congo	16	Montano et al. 2011
	Angola	138	Melo et al. 2011
Southern Africa	Mozambique	82	Alves et al. 2003
	Tanzania	143	Tishkoff et al. 2007
	Namibia	47	Fujihara et al. 2009
Madagascar	Madagascar	63	Tofanelli et al. 2009

Appendix B: MtDNA haplotypes and haplogroups found in Honduras, Roátan, St. Vincent, Dominica, and Belize.

Table B.1 MtDNA HVS-I and HVS-II haplotypes and haplogroups from the village of Cristales in Trujillo, Honduras.

ID	Hg	HVS I (nps 16025-16400) +16000	HVS II (nps 81-400)
CR02	L0	124, 223	152, 198, 199, 263, 309.1C, 315.1C
CR03	L0	124, 223	90.1G, 152, 198, 199, 263, 309.1C. 315.1C
CR04	L0	124, 223	152, 198, 199, 263, 309.1C, 315.1C
CR05	L0	35, 124, 223	152, 198, 199, 263, 309.1C, 315.1C
CR06	L0	241, 189, 223, 258C, 293C	125, 198, 199, 263, 309.1C, 315.1C
CR07	L0	124, 189, 223	152, 198, 199, 263, 309.1C. 315.1C
CR24	L0	223, 294, 309, 390	146, 452, 195, 198, 263, 315.1C
CR08	L1b1	126, 187, 189, 223, 264, 270, 293, 311	152, 182, 185, 189, 195, 198, 247, 263, 315.1C
CR09	L1b1	126, 187, 189, 223, 264, 270, 293, 311	81T, 150, 152, 189, 195, 198, 200, 263, 315.1C, 316, 366
CR10	L1b1	126, 187, 189, 223, 264, 270, 293, 311	152, 182, 185, 189, 195, 198, 247, 263, 309.1C, 315.1C, 357
CR11	L2	223, 294, 309, 368, 390	152, 182, 185, 189, 195, 198, 263, 315.1C, 357
CR12	L2	189, 192, 223, 294, 309, 390	81T, 143, 146, 152, 195, 198, 263, 309.1C, 315.1A
CR13	L2	189, 192, 223, 294, 309, 390	143, 146, 152, 195, 198, 263, 309.1C, 315.1C
CR14	L2a1	223, 294, 309, 368, 390	146, 152, 195, 198, 263, 315.1C
CR15	L2a1	223, 294, 309, 368, 390	152, 195, 198, 263, 315.1C
CR16	L2a1	223, 294, 309, 368, 390	146, 152, 195, 198, 263, 315.1C
CR17	L2a1	223, 294, 309, 368, 390	146, 152, 195, 198, 263, 315.1C
CR18	L2a1	223, 294, 309, 368, 390	146, 152, 195, 198, 263, 315.1C
CR19	L2a1	223, 294, 309, 390	143, 146, 152, 195, 198, 263, 315.1C,
CR20	L2a1	223, 264, 390	125G, 146, 150, 182, 195, 263, 309.1C, 315.1C, 325
CR21	L2a1	223, 294, 309, 390	143, 146, 152, 195, 198, 263, 315.1C
CR01	L3d	124, 223	152, 198, 199, 263, 309.1C. 315.1C
CR22	L3e1	176, 223, 311, 327	150, 152, 189, 198, 200, 263, 315.1C
CR23	L3e1	176, 223, 310, 311, 327	150, 152, 189, 198, 263, 315.1C
CR25	Unk	189, 192, 223, 294, 304A, 309, 390	143, 146, 152, 195, 198, 263, 309.1, 315.1C

Mutations are transitions unless noted by the base substituted. Deleteions are represented by the letter d. Insertions are noted by .1, or .2.

Table B.2 MtDNA HVS-I and HVS-II haplotypes and haplogroups from the village of Punta Gorda, Roátan.

ID	Hg	HVS I (nps 16025-16400) +16000	HVS II (nps 81-400)
PG01	A2	290, 319, 362	146, 152, 153, 235, 263, 309.1C, 315.1C
PG02	L0	51, 223, 278, 362	81.1A, 263, 315.1C
PG03	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 236, 247, 263, 309.1C, 315.C, 324G
PG04	L1	124, 187, 189,223, 264, 270, 278, 293, 311	152, 182, 195, 247, 263, 315.1C, 357
PG06	L1b	126, 187, 189, 223, 264, 270, 278, 311	151, 152,282, 185T, 189, 247, 263, 309.1C, 309.2C, 315.1C, 357, 366
PG19	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	152, 182, 185, 189, 195, 247, 263, 315.1C, 357
PG05	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	80C, 152, 182, 185, 195, 198, 263, 309.1C, 315.1C
PG07	L1b1	126, 187, 223, 264, 270, 278, 293, 311	152, 182, 185, 189, 195, 263, 315.1C, 357
PG08	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 312	152, 182, 185, 189, 195, 247, 263, 315.1C, 358
PG09	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	152, 182, 185T, 195, 247, 263, 309.1C, 315.1C, 357
PG10	L1c0	129, 172, 184, 187, 189, 223, 261, 278, 290, 293, 311, 360	151, 152, 182, 186, 189, 195, 198, 247d, 263, 265, 297, 315.1C, 316
PG11	L1c0	129, 172, 184, 187, 189, 223, 261, 278, 290, 293, 311, 361	151, 152, 182, 186, 189, 195, 198, 247d, 263, 265, 297, 315.1C, 317
PG12	L1c0	129, 172, 184, 187, 189, 223, 261, 278, 290, 293, 311, 360	151, 152, 182, 186, 189C, 195, 198, 247d, 263, 265, 297, 315.1C, 316
PG13	L1c0	129, 172, 084, 187, 189, 223, 261, 278, 290, 293, 311, 360	151, 152, 182, 186, 189C, 195, 198, 247d, 263, 265, 297, 315.1C, 316
PG14	L1c0	129, 172, 184, 187, 189, 223, 261, 278, 290, 293, 311, 360	151, 152, 182, 186, 189C, 195, 198, 247d, 263, 265, 297, 315.1C, 316
PG15	L1c0	129, 172, 184, 187, 189, 223, 261, 278, 290, 293, 311, 360	151, 152, 182, 186, 189C, 195, 198, 263, 297, 315.1C, 316
PG16	L1c0	129, 172, 184, 187, 189, 223, 261, 278, 290, 293, 360	151, 152, 182, 186, 189, 195, 198, 247d, 263, 265, 297, 315.1C, 316
PG17	L2a	223, 278, 294, 390	152, 182, 185T, 189, 195, 247, 263, 315.1C, 357
PG18	L2a1	189, 192, 223, 278, 294, 309, 390	81.G, 85.G, 143, 146, 152, 195, 263, 309.1C, 315.1C
PG20	L2c	230, 264, 278, 390	125G, 146, 150, 182, 195, 198, 263, 309.1C, 315.1C, 325
PG21	L2c	223, 264, 278, 390	146, 150, 182, 195, 198, 263, 315.1C, 324
PG22	L2c	223, 264, 278, 390	146, 150, 151, 182, 195, 198, 263, 309.1C, 315.1C, 325
PG46	L2c	223, 264, 270, 390	125G, 150, 182, 195, 198, 263, 309.1C, 315.1C, 325
PG48	L2c/d	223, 264, 278, 390	80G, 146, 150, 182, 195, 198, 263, 309.1C, 315.1C, 321, 325, 334. 341T. 344, 352
PG23	L2c2	94, 264, 266, 278, 390	146, 150,152, 182, 183, 195, 198, 263, 315.1C
PG37	L3	223, 311	80G, 143, 146, 152, 182, 189, 195, 200, 263, 309.1C, 315.1C, 379
PG24	L3e1	166, 185, 311, 327	81.aA, 90.aG, 96d, 150, 152, 185T, 189, 200, 263, 315.1C, 366,
PG25	L3e1	166, 185, 223, 311, 327	150, 152, 185, 189, 200, 263, 315.1C
PG26	L3e1	166, 185, 223, 311, 327	81d, 150, 185, 189, 200, 263, 315.1C
PG27	L3e1	166, 185, 223, 311, 327	150, 185, 189, 200, 263, 315.1C
PG28	L3e1	166, 185, 223, 311, 327	150, 152, 185, 189, 200, 263, 315.1C
PG29	L3e1	166, 185, 223, 311, 327	140G, 141G, 150, 185, 189, 200, 263, 315.1C
PG30	L3e1	166, 185, 223, 311, 327	150, 152, 185, 189, 198, 200, 263, 315.1C, 324, 357, 366, 369A
PG31	L3e1	168, 185, 223, 311, 327	150, 152, 185, 189, 200, 263, 315.1C, 366
PG32	L3e1	176,189, 223, 311, 327	150, 152, 189, 200, 263, 315.1C
PG33	L3e1	166, 185, 223, 311, 327	80G, 81, 150, 152, 185, 189, 200, 263, 315.1C
PG34	L3e1	185, 223, 311, 327	150, 152, 185, 189, 200, 263, 315.1C
PG35	L3e1	176, 223, 311, 327, 362	150, 152, 189, 200, 263, 315.1C,
PG36	L3e1	166, 185, 230, 311, 327	80G, 81, 85.1G, 150, 185, 189, 200, 263, 315.1C
PG38	L3e1	166, 185, 223, 311, , 327	150, 152, 189, 200, 263, 309.1A, 310, 311A, 316, 375G, 381A
PG39	L3e1	123A, 168, 185, 230, 327	80G, 150, 152, 189, 200, 263, 315.1C
PG40	L3e1	189, 223, 264, 270, 278, 311	152, 182, 185T, 189, 195, 263, 309.1C, 315.1C, 366
PG41	L3e1	168, 185, 223, 311, 327	150, 185, 189, 200, 263, 315.1C
PG42	L3e1	126, 185, 223, 311, 327	150,152, 189, 200, 263, 315.1C
PG43	L3e1	166, 185, 223, 311, 327	151, 152, 182, 186, 189, 195, 198, 247d, 263, 265, 297, 315.1C, 316
PG44	L3e1	166, 185, 223, 311, 327	150, 152, 185, 189, 200, 263, 315.1C
PG45	L3e1	166, 185, 223, 311, 327	150, 152, 185, 189, 200, 263, 315.1C
PG47	Unk	126, 187, 189, 223, 264, 270, 278, 293, 311	151, 152, 182, 186, 189C, 195, 198, 247d, 263, 265, 297, 315.1C, 316

Mutations are transitions unless noted by the base substituted. Deleteions are represented by the letter d. Insertions are noted by .1, or .2.

Table B.3. MtDNA HVS-I and HVS-II haplotypes and haplogroups from the village of Rio Negro in Trujillo, Honduras.

ID	Hg	HVS I (nps 16025-16400) +16000	HVS II (nps 81-400)
RN02	L0	74, 129, 145, 223, 391	152, 199, 204, 207, 263, 309.1C, 315.1C
RN03	L0	74, 129, 145, 223	152, 199, 204, 207, 263, 309.1C, 315.1C
RN04	L0	74, 129, 145, 223, 391	152, 199, 204, 207, 263, 309.1C, 315.1
RN05	L0	74, 129, 145, 223, 391	152, 199, 204, 207, 263, 309.1C, 315.1C
RN34	L0	189, 223, 362	146, 150, 195, 263, 315.1C, 324, 357C
RN06	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	90.1G, 142A, 152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C
RN07	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	96d, 142A, 146, 152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C
RN08	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	141G, 142d, 152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C
RN09	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C
RN10	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C, 324G, 366
RN11	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	105A, 152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C, 366
RN12	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 315.1C, 324G, 362A
RN13	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	80G, 81, 85.1G, 141d, 142A, 152, 189, 204, 247, 263, 309.1C, 315.C
RN14	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C, 324G, 376C
RN15	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C
RN16	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 309.2C, 315.1C, 332, 362C, 366
RN17	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1, 315.1C
RN18	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 321	96d, 152, 189, 204, 207, 236, 247, 263, 309.1, 315.1C
RN19	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C
RN20	L0a2	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C
RN21	L0a2	148, 172, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C, 366
RN22	L0a2	148, 172, 187, 188G, 189C, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C
RN23	L1b1	126, 187, 189, 223, 270, 278, 293, 311	152, 182, 185, 189, 195, 247, 263, 315.1C, 357
RN24	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	105A, 152, 182, 185T, 189, 195, 247, 263, 315.1C, 357
RN25	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
RN33	L2a1	223, 278, 294, 309	146, 152, 195, 263, 315.1C
RN26	L2c	223, 261, 278, 390	*125G, 129A, 146, 150, 195, 198, 263, 309.1C, 315.1C
RN27	L2c	223, 264, 278, 390	96d, 146, 150, 182, 195, 198, 263, 304G, 309.1C, 315.1C, 325, 379
RN28	L2c	223, 264, 278, 390	80G, 125G, 142G, 144A, 146, 150, 182, 195, 198, 263, 309.1C, 315.1C, 214, 366
RN29	L2c	35, 223, 264, 278, 390	125, 146, 150, 182, 195, 198, 263, 309.1C, 310, 315.1C, 321G, 325, 376C, 379C
RN30	L2c2	189, 223, 264, 278, 390	125G, 146, 150, 182, 195, 198, 263, 309.1C, 315.1C, 325
RN01	L3d	124, 223	152, 199, 263, 309.1C, 315.1C
RN31	L3e1	176, 223, 311, 327	150, 152, 189, 200, 263, 315.1C
RN32	L3e1	176, 189, 223, 311, 327	150, 152, 189, 200, 263, 315.1C

Mutations are transitions unless noted by the base substituted. Deleteions are represented by the letter d. Insertions are noted by .1, or .2.

* HVS-II haplotype begins at np 85.

Table B.4. MtDNA HVS-I and HVS-II haplotypes and haplogroups from the village of Santa Fe, on the Honduran Coast.

ID	Hg	HVS I (nps 16025-16400) +16000	HVS II (nps 81-400)
SF26	L0	129, 183C, 189, 258C, 256C, 278, 293C	46, 50, 195, 263, 315.1C
SF27	L0	189, 232	90.1G, 125G, 146, 150, 152, 189, 263, 315.1C, 317, 327, 338A, 348G, 353, 366, 398G
SF01	L1	126, 189, 223, 264, 270, 278, 293, 311	152, 182, 185T,189 195, 247, 263, 315.1C, 357
SF02	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	152, 182, 185T, 189, 195, 247, 263, 309.1C, 315.1C
SF03	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	152, 182, 185T,189 195, 247, 263, 315.1C, 358
SF04	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	152, 182, 189, 195, 247, 263, 308G, 315.1C, 357
SF05	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	152, 182, 185T, 189, 195, 247, 263, 315.1C, 357
SF06	L1b1	126, 187, 189, 223, 264, 270, 278, 293, 311	152, 182, 185T, 189, 195, 247, 263, 309.1C, 315.1C, 357
SF25	L1b1	126, 187, 189, 223, 264, 270, 293, 311	152, 189, 195, 247, 263, 315.1C, 357
SF07	L1c1	129, 172, 184, 187, 223, 261, 278, 290, 293, 311, 360	151, 152, 182, 186, 189C, 195, 198, 247d, 263, 265, 297, 315.1C, 316
SF08	L2a	189, 223, 278, 294, 309	143, 146, 152, 195, 24263, 309.1C, 315.1C, 366
SF09	L2a	189, 223, 278, 294, 309, 390	146, 152, 195, 263, 269A, 309.1C, 315.1C, 326C, 366, 389
SF10	L2a	223, 278, 294, 390	143, 146, 152, 182, 189, 195, 263, 309.1C, 315.1C, 366, 379
SF11	L2a	189, 192, 223, 278, 294, 309, 390	143, 146, 152, 195, 263, 309.1C, 315.1C
SF12	L2a	189, 223, 278, 294, 309, 390	143, 146, 152, 195, 263, 309.1, 315.1C
SF13	L2a	223, 278, 294, 309, 368, 390	*141A, 142A, 142d, 143, 146G, 152, 195, 263, 315.1C
SF14	L2a	192, 223, 278, 294, 309, 390	143, 146, 152, 195, 263, 309.1C, 315.1C
SF15	L2a	223, 278, 294, 390	81.1G, 143, 146, 152, 182, 189, 195, 263, 309.1C, 315.1C
SF16	L2a1	189, 223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
SF17	L2c	223, 264, 278	125, 146, 150, 182, 195, 198, 263, 309.1C, 315.1C, 325
SF18	L3e1	166, 185, 223, 311, 327	150, 185, 189, 200, 263, 315.1C
SF19	L3e1	166, 185, 223, 311, 327	80G, 81, 84, 90.1G, 150, 185, 189, 200, 263, 315.1C
SF20	L3e1	166, 185, 223, 311, 327	80d, 142, 150, 185, 189, 200, 263, 315.1C
SF21	L3e1	166, 185, 223, 311, 327	80d, 150, 185, 189, 200, 263, 315.1C
SF22	L3e1	166, 185, 223, 311, 327	150, 185, 189, 200, 263, 315.1C
SF23	L3e1	166, 185, 189, 223, 311, 327	141A, 142d, 150, 185, 189, 200, 263, 315.1C
SF24	L3e1	166, 185, 189, 223, 311, 328	80d, 150, 185, 189, 200, 163, 315.1C

Mutations are transitions unless noted by the base substituted. Deleteions are represented by the letter d. Insertions are noted by .1, or .2.

* HVS-II haplotype begins at np 85.

Table B.5. MtDNA HVS-I and HVS-II haplotypes and haplogroups from Belize.

ID	Hg	HVS I (nps 16025-16400) +16000	HVS II (nps 81-400)
Bel47	C1	51, 189, 223, 293, 298, 311, 325, 327, 386	146, 150, 249d, 263, 290d, 291d, 309.1C, 309.2, 315.1C
Bel01	L0a2	148, 172, 187, 189, 223, 230, 311, 320	152, 189, 204, 207, 263, 309.1C, 315.1C
Bel02	L0a2	148, 172, 187, 189, 223, 230, 311, 320	152, 189, 204, 207, 263, 309.1C, 309.2, 315.1C
Bel03	L0a2	148, 172, 187, 189, 223, 230, 311, 320	152, 189, 204, 207, 263, 309.1C, 309.2, 315.1C
Bel04	L0a2	148, 172, 187, 189, 223, 230, 311, 320	152, 189, 204, 207, 263, 309.1C, 309.2, 315.1C
Bel05	L0a2	148, 172, 187, 189, 223, 230, 311, 320	152, 189, 204, 207, 263, 309.1C, 309.2, 315.1C
Bel06	L0a2	148, 172, 187, 189, 223, 230, 311, 320	142A, 152, 189, 204, 207, 263, 309.1C, 315.1C
Bel07	L0a2	148, 172, 187, 189, 223, 230, 311, 320	152, 189, 204, 207, 263, 309.1C, 309.2, 315.1C
Bel08	L0a2	148, 172, 187, 189, 223, 230, 311, 320	152, 189, 204, 207, 263, 309.1C, 309.2, 315.1C
Bel09	L1b1	126, 145, 187, 189, 220, 222, 270, 293, 311	152, 182, , 185, 195, 247, 263, 317, 358
Bel10	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185T, 189, 195, 247, 263, 309.1C, 358
Bel11	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 315.1C, 358
Bel12	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 309.1C, 315.1A, 358
Bel13	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 309.1C, 315.1C, 358
Bel14	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 309.1C, 315.1C, 358
Bel15	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 309.1C, 315.1C, 358
Bel16	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 315.1C, 358
Bel17	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 315.1C, 358
Bel18	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 315.1C, 358
Bel19	L1b1	126, 187, 189, 220, 222, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 315.1C, 358
Bel20	L1c0	129, 172, 184, 187, 189, 223, 261, 290, 293, 311, 360	151, 152, 182, 186, 189, 195, 198, 247, 263, 297, 315.1C, 317
Bel21	L1c0	129, 172, 184, 187, 193, 223, 261, 290, 293, 311, 360	151, 152, 182, 186, 189, 195, 198, 247, 263, 297, 315.1C, 317
Bel22	L2a	123, 294, 309, 368, 390	146, 152, 195, 263, 317
Bel23	L2a	189, 192, 223, 294, 309, 390	143, 146, 152, 195, 263, 309.1C, 315.1C
Bel24	L2a	189, 192, 223, 294, 309, 390	143, 146, 152, 195, 263, 309.1C, 315.1C
Bel25	L2a	189, 192, 223, 294, 309, 390	143, 146, 152, 195, 263, 309.1C, 315.1C
Bel26	L2a	223, 278, 294, 309, 368, 390	143, 146, 152, 195, 263, 309.1C, 315.1C
Bel27	L2a	223, 278, 294, 309, 368, 390	141, 146, 152, 195, 263, 309.1C, 315.1C, 317
Bel28	L2a	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel39	L2a	223, 278, 294, 309, 368, 390	*146, 152, 195, 263, 303, 304G, 308G, 309.1C, 315.1C
Bel40	L2a	223, 278, 294, 309, 368, 390	83A, 146, 152, 195, 263, 315.1C
Bel41	L2a	223, 278, 294, 390	152, 182, 189, 195, 263, 309.1C, 309.2C
Bel29	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel30	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel31	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel32	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel33	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel34	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel35	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel36	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel37	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel38	L2a1	223, 278, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
Bel43	L3e1a	185, 223, 311, 327	150, 189, 200, 263, 315.1C
Bel44	L3e1a	185, 223, 311, 327	150, 189, 200, 263, 315.1C
Bel45	L3e1a	185, 223, 311, 327	150, 189, 200, 263, 315.1C
Bel46	L3e1a	185, 223, 311, 327	150, 189, 200, 263, 316
Bel42	L3f1	176, 209, 223, 311, 327	84, 150, 152, 189, 200, 263, 309.1C
Bel48	L3f1	129, 209, 223, 292, 295, 311	146, 152, 195, 263, 315.1C
Bel49	L3f1	129, 223, 295, 311	152, 189, 195, 200, 263, 309.1C, 315.1C
Bel50	L3f1	94, 129, 209, 223, 295, 311	152, 189, 195, 200, 263, 309.1C, 315.1C
Bel51	L3f1	94, 129, 209, 223, 295, 311	152, 189, 195, 200, 263, 309.1C, 315.1C
Bel52	L3f1	94, 129, 209, 223, 295, 311	152, 189, 195, 200, 263, 309.1C, 315.1C
Bel53	L3f1	94, 129, 209, 223, 295, 311	82T, 152, 189, 195, 200, 263, 309.1C, 315.1C
Bel54	W1g	148, 172, 187, 188G, 189, 223, 230, 311, 320	152, 189, 204, 207, 236, 247, 263, 309.1C, 315.1C, 320, 324, 362A,366, 391A

Mutations are transitions unless noted by the base substituted. Deleteions are represented by the letter d. Insertions are noted by .1, or .2.

* HVS-II haplotype begins at np 85.

Table B.6. MtDNA HVS-I and HVS-II haplotypes and haplogroups from St. Vincent.

ID	Hg	HVS I (nps 16025-16400) +16000	HVS II (nps 81-400)
SVG01	A2	111, 223, 278, 290, 319, 362	146, 153, 195, 235, 263, 315.1C
SVG02	A2	111, 223, 278, 290, 319, 362	146, 153, 195, 235, 263, 309.1C, 310, 311, 315.1C, 367
SVG03	A2	111, 223, 278, 290, 319	146, 153, 195, 235, 263, 315.1C
SVG04	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
SVG05	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 310, 311, 315.1C, 367
SVG06	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
SVG07	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 310, 311, 315.1C, 367
SVG08	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 311, 315.1C, 367
SVG09	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 311, 315.1C
SVG10	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
SVG11	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
SVG12	C1	223, 278, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
SVG30	C1	223, 278, 298, 325, 327	80G, 249d, 263, 290d, 291d, 309.1C, 310, 315.1C, 321G
SVG13	L1b1	126, 187, 189, 223, 264, 270, 293, 311	152, 182, 185, 189, 195, 247, 263, 315.1C, 317A, 358
SVG23	L2a	189, 192, 223, 294, 309, 390	146, 195, 263, 315.1C
SVG24	L2a	110, 223, 294, 309, 390	143, 146, 152, 195, 263, 309.1C, 315.1C
SVG25	L2a	189, 192, 223, 291, 309, 390	185, 189, 200, 236, 247, 263, 309.1C, 310
SVG19	L2a	223, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
SVG14	L2a1	223, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
SVG15	L2a1	223, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
SVG16	L2a1	223, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
SVG17	L2a1	189, 192, 223, 294, 309.1C, 390	146, 152, 195, 263, 309.1C, 315.1C
SVG18	L2a1	223, 294, 309, 368, 390	146, 152, 195, 263, 315.1C
SVG20	L2a1	189, 192, 223, 294, 309	146, 152, 195, 263, 315.1C
SVG21	L2a1	223, 294, 309, 368, 390	*146, 152, 195, 263, 315.1C
SVG22	L2a1	223, 286, 294, 309, 390	143, 146, 152, 195, 263, 309.1C, 315.1C
SVG26	L2b	114, 129, 213, 223, 325, 390	146, 150, 152, 182, 183, 195, 198, 204, 263, 315.1C
SVG27	L2e	111A, 145, 184, 192, 223, 292, 390	146, 150, 152, 182, 263, 309.1C, 310, 315.1C
SVG28	L3b	124, 223G, 362	146, 263, 309.1C, 315.1C
SVG29	L3b	124, 223G	263, 315.1C

Mutations are transitions unless noted by the base substituted. Deleteions are represented by the letter d. Insertions are noted by .1, or .2.

* HVS-II haplotype begins at np 90.

Table B.7. MtDNA HVS-I and HVS-II haplotypes and haplogroups from the Kalinago in Dominica.

ID	Hg	HVS I (nps 16025-16400) +16000	HVS II (nps 81-400)
Dom21	A2	111, 176, 194, 223, 290, 291, 319	146, 153, 235, 263, 309.1C, 315.1C
Dom22	A2	83, 111, 223, 256	146, 152, 153, 214, 235, 263, 309.1C, 315.1C
Dom23	A2	83, 111, 223, 256, 290, 319	146, 152, 153, 214, 235, 263, 309.1C, 315.1C
Dom24	A2	83, 111, 223, 256, 290, 319	146, 152, 153, 214, 235, 263, 309.1C, 315.1C
Dom25	A2	84, 111, 194, 223, 290, 319	146, 153, 235, 263, 315.1C
Dom17	C1	51, 223, 298, 325, 327	105, 209, 249d, 263, 290d, 291d, 303, 309.1C, 315.1C
Dom26	C1	51, 189, 223, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom27	C1	51, 194, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom28	C1	51, 194, 223, 298, 325, 327	82, 249d, 263, 290d, 291d, 309.1C, 315.1C
Dom29	C1	51, 223, 298, 325, 327	82T, 249d, 263, 290d, 291d, 309.1C, 315.1C
Dom30	C1	51, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom31	C1	51, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 310, 315.1C
Dom32	C1	51, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom33	C1	51, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom34	C1	51, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom35	C1	51, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom36	C1	51, 223, 298, 325, 327	81, 82, 85C, 101C, 105, 249d, 263, 290d, 291d, 309.1C, 315.1C
Dom37	C1	51, 223, 298, 325, 327	81.1T, 83A, 249d, 263, 290d, 291d, 309.1C, 315.1C
Dom38	C1	51, 223, 298, 325, 327	83d, 249d, 263, 290d, 291d, 309.1C, 315.1C, 321G, 380
Dom39	C1	51, 223, 298, 325, 327	105, 249d, 263, 290d, 291d, 309.1C, 315.1C
Dom40	C1	51, 223, 298, 325, 327	98, 249d, 263, 290d, 291d, 309.1C, 315.1C
Dom41	C1	51, 223, 291, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom42	C1	152, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C, 380
Dom43	C1	152, 223, 298, 325, 327	81, 125A, 249d, 263, 290d, 291d, 309.1C, 315.1C
Dom44	C1	152, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1, 315.1C
Dom12	C1	51, 189, 209, 223, 258, 291, 298, 325, 327, 386A	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom53	C1	51, 189, 223, 258, 291, 298, 325, 327	249d, 263, 290d, 291d 309.1C, 315.1C
Dom01	C1	51, 110, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom05	C1	51, 189, 223, 258, 265, 291, 293, 298, 325, 327, 386	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom08	C1	223, 298, 325, 327	185, 249d, 263, 290d, 291d, 309.1C, 315.1C
Dom02	C1	51, 223, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom06	C1	51, 189, 209, 223, 258, 263, 291, 293, 298, 325, 327	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom16	C1	51, 189, 209, 223, 258, 291, 298, 325, 327, 386A	249d, 263, 290d, 291d, 309.1C, 315.1C
Dom20	C1	51, 223, 298, 325, 327	249d, 263, 290d, 291d, 263, 309.1C, 315.1C
Dom46	L1b	187, 189, 223, 264, 270, 278, 311	151, 152, 182, 185, 195, 200, 247, 263, 315.1C, 358
Dom09	L1c1	129, 187, 189, 223, 256, 278, 284, 293, 294, 311, 360	151, 152, 182, 186, 195, 198, 247, 263, 297, 309.1C, 315.1C
Dom11	L1c1	129, 187, 189, 223, 278, 284, 293, 294, 311	151, 152, 182, 186, 195, 198, 247, 263, 297, 309.1C, 315.1C, 317
Dom45	L1c1	129, 187, 189, 223, 256, 278, 284, 293, 294, 311	151, 152, 182, 186, 195, 198, 247, 263, 309.1C, 315.1C, 317, 367
Dom10	L1c1	129, 187, 189, 223, 256, 278, 284, 293, 294, 311, 360	151, 152, 182, 186, 189, 195, 198, 247, 263, 267, 309.1C, 315.1C, 316, 366, 376
Dom47	L2a	126, 192, 223, 278, 294, 309	146, 152, 195, 263, 309.1C, 315.1C
Dom03	L2a1	192, 264, 278, 294, 390	143, 146, 152, 195, 263, 315.1C
Dom48	L2b	114A, 129, 213, 223, 278	150, 152, 182, 195, 198, 204, 263, 309.1, 315.1C
Dom52	L3b/d	124, 223, 291	152, 263, 309.1C, 315.1C
Dom51	L3d	124, 223, 256, 319	152, 263, 315.1C
Dom04	L3e2	172, 183, 188, 189, 223, 320	150, 195, 263, 315.1C
Dom13	L3e2	172, 183, 188, 189, 223, 320	150, 195, 263, 315.1C
Dom14	L3e2	172, 183, 188, 189, 223, 320	88, 105, 150, 195, 263, 304, 315.1C, 317, 380
Dom15	L3e2	172, 183, 188, 189, 223, 320	150, 195, 198, 263, 315.1C
Dom49	L3e2	172, 183C, 188, 189, 320	150, 195, 263, 315.1C
Dom50	L3e2	172, 183C, 188, 189, 223, 320	150, 195, 263, 315.1C
Dom07	unk	27, 30d, 129, 187, 189, 223, 278, 284, 293, 294, 311, 360	151, 152, 182, 186, 189, 195, 198, 247, 263, 297, 315.1C, 316

Mutations are transitions unless noted by the base substituted. Deleteions are represented by the letter d. Insertions are noted by .1, or .2.

Appendix C: Y Haplogroup Networks for haplogroups E1b1 and Q.

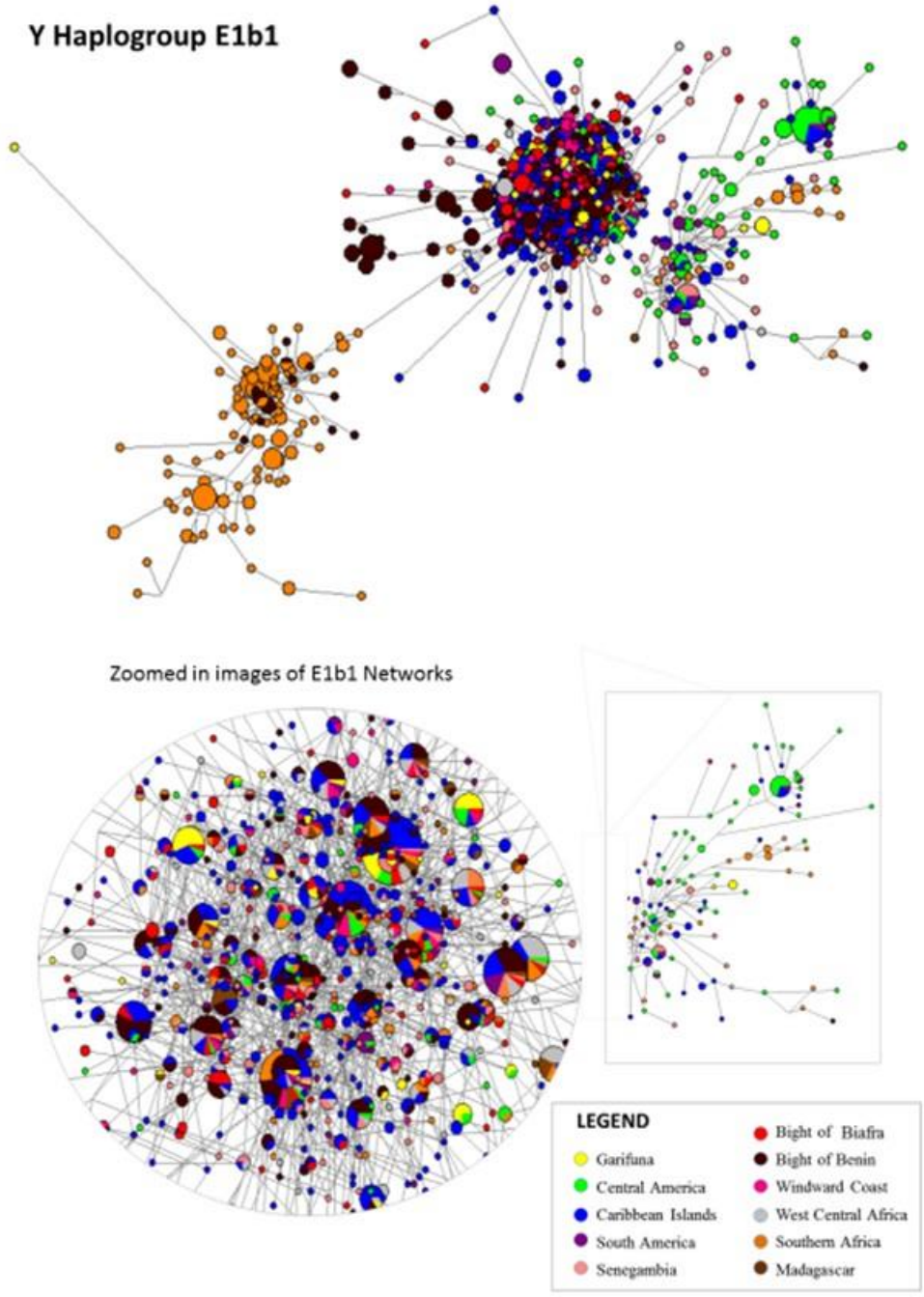

Figure C.1. Y haplogroup Network E1b1 for Garifuna villages and all comparative data.

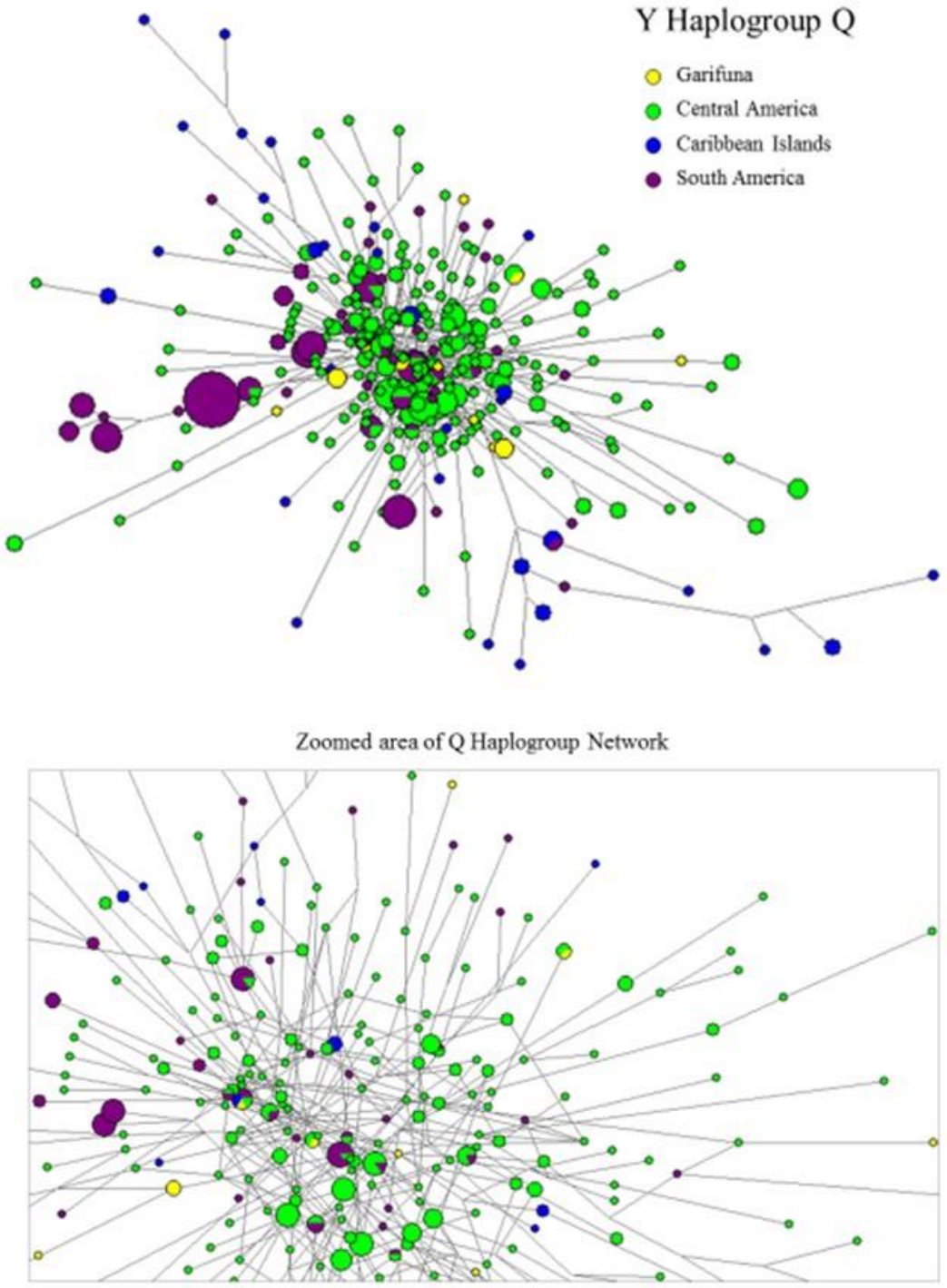

Figure C.2. Y haplogroup Q Network for Garifuna and all comparative data included in this study.